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VOLUME 16, NO. 1 MAY 1947

THE SOIL FAUNA OF TWO CONTRASTED PLOTS OF LAND IN TRINIDAD, BRITISH WEST INDIES

BY A. H. STRICKLAND

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1. INTRODUCTION

Population studies of the arthropod fauna of the soil have been receiving a considerable amount of attention of late in temperate regions, largely owing to the existence of a number of important insect pests that spend varying periods of their life cycles in the soil. Few such studies have, however, been carried out in the tropics, and it is for this reason that the writer decided to spend as much time as could be spared on an investigation of the soil fauna in Trinidad.

Part of this work has already been published (Strickland, 1945), and the present paper details the results so far unpublished. These consist of six series of samples taken on two contrasted plots over a period of three months (23 November 1943–1 March 1944), and deals principally with the fluctuations in population encountered as the wet season draws to a close, and the dry season sets in.

2. METHODS

(*a*) *Sampling.* Samples were taken in the form of cores 3·6 in. in diameter, at two depths, 0–1½ and 1½–3 in. Five of these samples were taken at random on each plot on each of the six occasions on which the plots were visited; in the case of the cacao plot, the surface litter was removed first, and treated as a separate sample. The five litter samples were bulked and placed in a tin, and the two depths of soil samples likewise bulked and placed in tins for removal to the laboratory for extraction. Two slivers of soil—corresponding to the two depths of sample—were removed from the sides of each auger hole for soil moisture determinations.

(*b*) *Extraction.* Five Berlese-Tullgren funnels (Tullgren, 1917) were used to extract the fauna from the soil samples. It was found that a 60 W. electric light bulb suspended 10 in. above the level of the soil when the funnels were full would dry out the soil almost completely in five days. After six days the soil was removed from the funnels and examined carefully with a hand lens, when any animals too large to migrate through the mosquito gauze fitted to the funnels were removed and preserved. One series of samples, after extraction in this manner, was put through the washing apparatus used in the first series of investigations, and no further animals were found.

After the funnels had been filled, the tins, in which the samples were carried to the laboratory, were washed out with alcohol, and any animals remaining in them collected, and added to the total collection for that particular series of samples. With the soil samples, up to 7% of the population was obtained, and from one of the litter samples, 12% of the animals were found, in these tin washings.

Two major objections have been raised to the use of Berlese-Tullgren funnels for extracting quantitative soil samples. Jacot (1936) points out that small insects may get trapped inside baked lumps of soil, and consequently be missed when the animals are being counted, and Trägårdh (1933) maintains that '...the biocoenoses of different biotopes differ so greatly in composition and reaction towards light and low humidity that it is quite impossible to draw any conclusions from one sample concerning the treatment of another'. It is the writer's opinion that neither of these objections is valid in the present case. The soil on both plots was a detrital silt of very light texture. When dried out it tended to form dust rather than large lumps. It is therefore maintained that the quantitative results from both plots are comparable amongst themselves, though not necessarily to, say, heavy clay samples extracted in the same manner.

3. THE AREAS SAMPLED

Two contrasted plots, one under the relatively sheltered environment of a cacao plantation, and the other under the exposed conditions of savannah land, were sampled at fortnightly intervals during the last

month of the wet season in 1943, and the first two months of the dry season of 1943–4, with the object of determining any major changes in the soil fauna that might occur as the soil dries out.

The cacao plot. Fifteen years ago the Department of Botany of the Imperial College of Tropical Agriculture took over a 5-acre block of land in the foothills of the Northern Range of Trinidad, near the St Augustine Cotton Experimental Station. Twelve years ago the plot was planted up with various types of Trinidadian and Ecuadorean cacao (*Theobroma cacao* L.), a few immortelles (*Erythrina* spp.) being put in at the same time to provide shade. During the past twelve years, the plot has been entered occasionally by labourers and college staff harvesting the crop, and taking measurements, but apart from these infrequent incursions, has remained undisturbed. At the time the samples were taken the cacao and immortelle trees were about 12 ft. high, just coming into full bearing, and providing a thick overhead canopy such that the litter and soil surface never felt the direct rays of the sun, except in occasional 'flecks' where the canopy had been broken owing to the loss of a branch.

The savannah plot. This plot, with the exception of a quarter of an acre in the north-east corner (on which some fertilizer trials had been carried out in 1939) had been down to permanent savannah grass for many years. It was in many respects similar to a well-kept English pasture. At the time the samples were taken, it had been absolutely untouched (apart from the routine fortnightly mowing) for at least four years. It was completely unshaded at all times of the day, and thus exposed to the full strength of the sun and rain.

This plot was sampled in two ways: first, the usual five cores were taken at random over the whole plot, and secondly, a subplot, 25 sq. yd. in area, and situated precisely in the middle of the whole plot, was pegged out and sampled at the same time as the whole plot. The grass was allowed to grow on this subplot, whereas the routine mowing was carried out over the rest of the plot. Some idea could therefore be gained of the buffering effect exerted by tall grass on the soil-inhabiting animals at the height of the dry season. The soil, a northern range detrital silt, was the same on both the cacao and savannah plots. The moisture fluctuations over the sampling period are given in Table 1.

Table 1. *Soil moistures in per cent*

Sample ...		1	2	3	4	5	6
Cacao plot	0–1½ in.	38·8	31·2	39·0	37·6	38·6	31·7
	1½–3 in.	37·7	29·8	34·0	32·5	33·3	27·4
Savannah whole plot	0–1½ in.	25·9	32·6	43·3	39·1	28·1	16·0
	1½–3 in.	22·1	26·7	32·8	29·1	24·1	16·5
Savannah subplot	0–1½ in.	27·8	29·2	41·5	45·9	27·8	22·1
	1½–3 in.	25·0	23·2	30·0	31·7	33·9	21·4

Table 2. *Meteorological data for both plots*

		Cacao			Savannah		
Month	Week	Rainfall (in.)	Mean % min. humidity	Soil temp. ° F.	Rainfall (in.)	Mean % min. humidity	Soil temp. ° F.
November	2	?	74	76·9	1·12	66·7	73·9
	3	?	63	76·6	0·70	51·6	74·4
	4	?	70	77·0	1·96	60·0	74·1
December	1	1·16	68	77·3	0·84	60·7	74·1
	2	1·08	68	76·5	1·12	63·7	73·9
	3	1·38	65	76·4	1·40	60·9	73·0
	4	0·60	60	75·2	0·56	56·3	71·0
January	1	1·73	66	76·9	1·68	60·1	72·4
	2	0·24	59	76·9	0·24	54·1	73·6
	3	0·87	51	75·8	0·42	53·9	71·9
	4	0·11	53	75·2	0·02	51·4	71·9
February	1	0·46	56	76·6	0·16	54·6	72·0
	2	0·06	51	75·3	0·08	51·3	71·3
	3	0·33	57	74·6	0·36	47·4	70·9
	4	0·02	43	74·3	0·01	43·6	70·4

Weekly rainfall, humidity, and soil temperature readings for both plots are given in Table 2.

The soil temperature (at a uniform depth of 1½ in. below the soil surface) does not vary more than 4° F.

in either plot, but the cacao plot has consistently higher temperatures and humidity than the savannah plot. The rainfall for both plots is much the same, which is not surprising since they were less than a mile apart.

4. RESULTS

The results obtained from these series of samples are given in Check Lists 1 and 2, and Tables 3, 4 and 5. For convenience, the check lists have been split up into groups, and a few notes on the determinations added at the end of each group. The specialists, to whom the writer is indebted for most of the determinations, are referred to individually in § 7.

(*a*) *The qualitative results*

Check List 1. *Arthropod fauna of the cacao plot*

CRUSTACEA.

Terrestrial isopods of the family ONISCIDAE were present in small numbers. It has not been possible to have them identified generically.

MYRIAPODA.

Diplopoda. POLYZONIDAE: *Siphonotus purpureus* Pocock.

Chilopoda. CRYPTOPIDAE: *Newportia oligopla* Chamberlin.

Only two species were present amongst the 49 myriapods in the cacao plot samples. Of these 35 were of the *Newportia*.

INSECTA.

Thysanura. JAPYGIDAE: *Parajapyx* sp.

Only one species of Thysanuran was present.

Collembola. PODURIDAE: Pseudachorutinae, two undetermined genera. ISOTOMIDAE: *Isotoma minor* Schaffer, *Folsomides* sp., *Proisotoma* sp. ENTOMOBRYIDAE: *Cyphoderus* sp., *Campylothorax* sp., *Entomobrya* sp., *Lepidocyrtinus* sp., *Lepidocyrtus* sp. SMINTHURIDAE: Sminthurinae, one genus not determined.

The commonest springtail was the *Proisotoma* sp. The two genera of Podurids were next in frequency of occurrence, being followed by the *Lepidocyrtus* sp., *Isotoma minor* and *Folsomides* sp. The other species occurred in small numbers only. All of the material has been retained at the Bureau of Entomology in Washington, U.S.A. for further study.

Thysanoptera. THRIPIDAE: *Frankliniella insularis* Frankl. PHLOEOTHRIPIDAE: *Zeugmatothrips* sp., *Hoplandothrips* sp., *Adraneothrips* sp.

The *Frankliniella* was the commonest thrips present, the samples taken in February 1944 containing large numbers of nymphs of this species. It seems likely that they were feeding on cacao rootlets, since the plot was virtually free of weed growth at the time the samples were taken.

Psocoptera. PSOCIDAE: *Ectopsocus* sp., and one undetermined species. TROGIIDAE: *Liposcelis* sp., and one undetermined species. PSOQUILLIDAE: *Psocatropos* sp.

The *Psocatropos* and *Liposcelis* species were present in about equal numbers, and together formed nearly 80% of the Psocoptera collected.

Hemiptera, Heteroptera. LYGAEIDAE: *Annomatocoris minutissima* China. VELIIDAE: *Microvelia mimula* B. White. CERATOCOMBIDAE: *Schizoptera* (*Odontorrhagus*) *stricklandi* China. ANTHOCORIDAE: *Lasiochilus variecolor* Uhler.

Hemiptera, Homoptera. JASSIDAE: *Thamnotettix colonus* Uhler. PSEUDOCOCCIDAE: *Rhizoecus moruliferus* Green, *Rhizoecus* sp. ORTHEZIIDAE: *Ortheziopa reynei* Laing.

The Lygaeid forms a new genus, which Dr China has described (in the Press). Dr China states (in litt.): '. . . it is completely without compound eyes or ocelli and is thus very remarkable as a hemipteron which is quite blind. I would say it is the only bug in your collection which is truly a subterranean species.' A number of Anthocorid nymphs were present in the samples. These may be the same species as the adults, but Dr China points out that it is impossible to be certain of this. Of the Coccids, the Ortheziids occurred in small numbers, the majority being Pseudococcids of the essentially hypogoeic genus *Rhizoecus*.

Coleoptera. STAPHYLINIDAE: *Oxytelus incisus* Motsch, *Oxytelus* sp., *Trogophloeus* sp., *Diochus nanus* Er., *Coprophilus pulchellus* Er., *C. rutila* Er., *Atheta* spp., Paederini, six species, two undetermined species. HISTERIDAE: *Hister* sp. SCAPHIDIDAE: *Scaphisoma* sp. SCYDMAENIDAE: *Eucomus* sp., *Scydmaenus* sp. PSELAPHIDAE: ? *Euplectus* sp. PTILIIDAE: *Ptilinum* sp. DRYOPIDAE, one undetermined species. NITIDULIDAE, PHALACRIDAE, CUCUJIDAE: one species of each family. ANTHICIDAE: *Anthicus* spp. APHODIDAE, CURCULIONIDAE: one species of each family. SCOLYTIDAE: two undetermined species. In addition to these adult beetles, larvae of the following families were present: STAPHYLINIDAE (Paederini spp.), PTILIIDAE, CANTHARIDAE (*Cantharis* sp.), ELATERIDAE (Elaterinae spp., Pyrophorinae, one species), PTILODACTYLIDAE, MYCETOPHAGIDAE, CUCUJIDAE, ?RHIZOPHAGIDAE, ANTHICIDAE, and CERAMBYCIDAE.

The commonest adult beetles were of the group Staphylinoidea (*Trogophloeus* sp., *Eucomus* sp., and *Atheta* spp.), 75% of the total Coleoptera belonging to this superfamily. The Curculionidae formed 20% of the total beetles. Staphylinid larvae, especially of the tribe Paederinae, were the commonest larval Coleoptera, followed closely by the Cucujoidea. The complete absence of Carabidae is interesting, and somewhat of a mystery.

Table 3. *Cacao plot. Faunal analysis*

Sampling dates ...	16 November				1 December				21 December				13 January				9 February				23 February				Grand
Sample ...	C. 1				C. 2				C. 3				C. 4				C. 5				C. 6				
	L.*	o–1½	1½–3	Total	L.	o–1½	1½–3	Total	L.	o–1½	1½–3	Total	L.	o–1½	1½–3	Total	L.	o–1½	1½–3	Total	L.	o–1½	1½–3	Total	total
Isopoda	—	—	—	—	3	4	—	7	7	7	—	14	—	13	—	13	1	2	—	3	—	15	10	25	62
Myriapoda	5	1	—	6	4	4	—	8	8	6	—	14	1	6	1	8	2	4	—	6	1	4	2	7	49
Arachnida (not Acarina)	32	12	2	46	14	9	7	30	9	3	1	13	5	14	3	22	6	14	1	21	5	21	16	42	174
Acarina	547	126	29	702	583	37	20	640	427	164	14	605	164	116	22	302	468	62	59	589	263	153	121	537	3375
Collembola	298	79	19	396	206	64	16	286	108	26	4	138	43	61	2	106	140	47	36	223	68	99	137	304	1453
Thysanura	1	1	—	2	—	1	1	2	—	1	—	1	—	—	—	—	—	1	—	1	—	1	—	1	7
Orthoptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Isoptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thysanoptera	1	—	—	1	1	—	—	1	—	—	—	—	5	9	3	17	145	10	6	161	52	17	19	88	268
Psocoptera	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	3	6	—	2	8	10	2	1	13	24
Hemiptera (nymphs)	—	2	1	3	—	—	—	—	—	—	3	3	—	—	—	—	2	1	—	3	4	1	1	6	15
Hemiptera (adults)	—	2	—	2	—	1	—	1	—	1	3	4	—	—	—	—	1	—	—	1	—	—	1	1	9
Hemiptera (Coccids)	1	2	—	3	5	—	—	5	1	—	—	1	1	1	1	3	—	1	1	2	—	3	—	3	17
Coleoptera (larvae)	10	5	—	15	13	2	—	15	7	—	—	7	—	—	1	1	15	2	9	26	15	8	2	25	89
Coleoptera (adults)	15	13	3	31	6	13	4	23	10	3	3	16	9	2	1	12	50	6	12	68	22	13	9	44	194
Diptera (larvae)	8	2	—	10	3	—	—	3	25	2	—	27	21	7	—	28	4	2	1	7	1	—	4	5	80
Diptera (adults)	—	5	—	5	1	—	1	2	1	—	—	1	2	—	3	5	2	—	1	3	1	—	—	1	17
Lepidoptera (larvae)	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	1
Lepidoptera (adults)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hymenoptera (not ants)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	2	—	—	2	3
Formicidae (larvae)	8	—	1	9	—	—	—	—	5	—	—	5	28	35	2	65	1	3	—	4	8	—	—	8	91
Formicidae (adults)	363	19	16	398	21	4	35	60	314	23	18	355	225	18	24	267	36	19	6	61	14	10	7	31	1172
Undetermined larvae	2	—	—	2	2	—	—	2	—	—	—	—	—	1	—	1	—	1	—	1	—	—	—	—	6
Totals	1291	269	71	1631	862	139	84	1085	922	236	46	1204	505	286	63	854	880	175	134	1189	466	347	330	1143	7106

* 'L.' denotes litter; o–1½, etc., depths of samples in inches.

Hymenoptera. BETHYLIDAE: *Trichopria* sp. FORMICIDAE. The ants were examined cursorily by the writer whilst sorting out the material, and were packed in tubes ready for dispatch to a specialist. It is most unfortunate that they were lost in transit, through enemy action. It is therefore only possible to give generic determinations of types well known to the writer. *Rhizomyrma* spp., *Solenopsis* spp., and a number of species of the tribe Attini formed the majority of the population. Species of *Pheidole*, *Ponera*, *Strumigenys* and *Brachymyrmex* were present in small numbers.

Diptera, Nematocera. PSYCHODIDAE: *Psychoda* sp. HELEIDAE: *Culicoides* sp., *Dasyhelea* sp., *Forcipomyia* sp. CECIDOMYIDAE: Genera indet. PHORIDAE: *Megaselia* sp. Larvae of the Nematocerous families CHIRONOMIDAE, HELEIDAE, the Brachycerous family STRATIOMYIDAE, and the Cyclorraphous family ANTHYOMYIDAE were present.

The commonest Diptera, adult and larval, were small Heleids. It is of interest to note the presence of *Forcipomyia* sp. adults in the litter samples. Species of this genus are thought by Posnette (1944) to be partly responsible for the natural pollination of cacao, and are therefore of some economic importance.

ARACHNIDA.

Araneae. OONOPIDAE: *Scaphiella cymballaria* Simon, *Stenoonops* sp. DYSDERIDAE: *Dysderina* sp. CLUBIONIDAE: *Corinna* sp. PHOLCIDAE: *Modisimus* sp. ULOBORIDAE: *Uloborus* sp. THERIDIIDAE: *Theridion* sp., *Mysmena* sp. LINYPHIIDAE: one undetermined species.

The commonest spiders were the species of *Dysderina* and *Stenoonops*, both probably new to science, and to be described by Dr Gertsch as time permits.

PEDIPALPI.

SCHIZOMIDAE: *Schizomus flavescens* Hansen & Sorensen.

One sub-adult male, and one nymph only.

CHELONITHIDA.

Heterosphyronida. CTHONIIDAE: *Tyrranochthonius insulae* Hoff, *Pseudochthonius heterodentatus* Hoff.

Diplosphyronida. OLPIIDAE: *Novohorus cinereus* Hoff, and *Neopachyolpium longum* Hoff.

The pseudoscorpions were all new to science, both of the Olpiids forming new genera (Hoff, 1945). The commonest species was the *Tyrranochthonius*, of which 78 specimens were taken—54 males, 18 tritonymphs and 6 deutonymphs. No females were found.

SCORPIONOIDEA.

Five immature scorpions were found in the samples. All were of the same species, and Dr Gertsch informs the writer that it is not possible to place them generically at present.

ACARINA.

CERATOZETIDAE: *Scheloribates* sp. CUNAXIDAE: *Cunaxa inermis* Trag. DAMEOSOMIDAE: *Dameosoma* sp. EUPODIDAE: *Linipodes* sp. GALUMNIDAE: *Galumna* sp., *Zetes* sp. HYPOCHTHONIDAE: *Hypochthonius* sp., *Trhypochthonius* sp. MACROCHELIDAE: *Macrocheles* sp. NEOLIODIDAE: *Neoliodes* sp. PARASITIDAE: *Parasitus* sp., *Hydrogamasus* sp., *Eugamasus* sp. PHTHIRACARIDAE: *Pseudotritia ardua* Koch. TRACHYUROPODIDAE: *Trachyuropoda* sp. UROPODIDAE: *Uropoda* sp., *Cilliba* sp.

At least 17 distinct species of mites were present in the cacao plot samples, and further examination of the material will almost certainly increase this number. As noted in the previous investigation, the Oribatids were by far the commonest inhabitants of the litter and top soil layer. It is of some interest that the genera found in the previous investigation do not coincide at all well with the present collection. In fact, only four families are common to both.

In the cacao plot, then, *at least* 16 orders, 75 families, and (excluding the ants) 120 species of arthropods were encountered. This estimate is almost certainly too low, and when the material has been thoroughly examined, will doubtless be increased considerably.

Check List 2. *Arthropod fauna of the savannah plot*

CRUSTACEA.

Three Oniscid isopods only were present in the savannah plot samples. It has not been possible to have them identified generically.

MYRIAPODA.

Chilopoda. BALLOPHILIDAE: *Leucolinum trinidadense* Chamberlin. HENICOPIDAE: *Lamyctinus coeculus* Brol., *Lamyctes* sp.

The absence of millipedes from the savannah plot is of some interest but, in view of their well-known liking for rich, moist forest soils, not really surprising.

INSECTA.

Thysanura. JAPYGIDAE: *Japyx* sp., *Parajapyx* sp.

Only two species. The *Parajapyx* was the same species as was found on the cacao plot.

Collembola. ISOTOMIDAE: *Proisotoma* sp., one undetermined species. ENTOMOBRYIDAE: *Cyphoderus* sp., *Lepidocyrtus* sp. SMINTHURIDAE: *Dicyrtomina* sp.

The Entomobryids were the commonest springtails present.

Orthoptera. GRYLLIDAE: *Gryllulus* sp.

Four nymphs only of this cricket were present.

Thysanoptera. THRIPIDAE: *Frankliniella trinidadensis* Hd., Thripinae, 1 sp., Sericothripinae, 1 sp.

Table 4. *Savannah plot. Faunal analysis*

Sampling dates ...	23 November			7 December			31 December			24 January			17 February			1 March			Grand
Sample ...	S. 1			S. 2			S. 3			S. 4			S. 5			S. 6			
	0–1½	1½–3	Total	0–1½	1½–3	Total	0–1½	1½–3	Total	0–1½	1½–3	Total	0–1½	1½–3	Total	0–1½	1½–3	Total	total
Isopoda	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Myriapoda	5	1	6	6	4	10	4	2	6	4	—	4	1	7	8	—	—	—	34
Arachnida (not Acarina)	—	—	—	1	—	1	—	1	1	2	—	2	—	—	—	—	—	—	4
Acarina	300	36	336	154	8	162	260	10	270	175	19	194	243	19	262	184	43	227	1451
Collembola	145	11	156	89	5	94	159	13	172	64	16	80	70	2	72	78	6	84	658
Thysanura	13	3	16	—	4	4	5	—	5	2	1	3	1	—	1	6	1	7	36
Orthoptera	1	—	1	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	2
Isoptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thysanoptera	2	—	2	—	—	—	1	1	2	2	—	2	4	—	4	13	3	16	26
Psocoptera	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	1
Hemiptera (nymphs)	1	—	1	3	—	3	17	—	17	2	—	2	1	—	1	—	—	—	24
Hemiptera (adults)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemiptera (Coccids)	11	5	16	22	—	22	30	1	31	—	—	—	9	2	11	2	2	4	84
Coleoptera (larvae)	5	1	6	2	1	3	—	—	—	4	5	9	2	—	2	2	1	3	23
Coleoptera (adults)	12	2	14	8	1	9	4	—	4	7	5	12	5	—	5	6	1	7	51
Diptera (larvae)	7	—	7	—	—	—	1	—	1	—	—	—	1	—	1	—	—	—	9
Diptera (adults)	1	2	3	—	—	—	2	2	4	—	2	2	1	—	1	—	1	1	11
Lepidoptera (larvae)	1	—	1	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	2
Lepidoptera (adults)	1	—	1	1	—	1	—	1	1	1	—	1	—	—	—	1	—	1	5
Hymenoptera (not ants)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1
Formicidae (larvae)	1	—	1	6	—	6	—	—	—	—	—	—	—	—	—	2	—	2	9
Formicidae (adults)	34	17	51	139	22	161	4	4	8	1	—	1	30	—	30	11	—	11	262
Undetermined larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Totals	540	78	618	431	45	476	488	35	523	265	48	313	368	31	399	306	58	364	2693

Table 5. *Savannah subplot. Faunal analysis*

Sampling dates ...	23 November			7 December			31 December			24 January			17 February			1 March			Grand total	Grand total for whole and sub-plots
Samples ...	S. 1/A			S. 2/A			S. 3/A			S. 4/A			S. 5/A			S. 6/A				
	0–1½	1½–3	Total	0–1½	1½–3	Total	0–1½	1½–3	Total	0–1½	1½–3	Total	0–1½	1½–3	Total	0–1½	1½–3	Total		
Isopoda	—	—	—	1	—	1	1	—	1	—	—	—	1	—	1	—	—	—	3	3
Myriapoda	24	4	28	14	3	17	9	5	14	16	1	17	17	—	17	25	12	37	130	164
Arachnida (not Acarina)	—	—	—	—	—	—	3	—	3	1	—	1	1	—	1	2	—	2	7	11
Acarina	497	34	531	556	13	569	340	6	346	598	37	635	603	82	635	357	55	412	3128	4579
Collembola	184	4	188	181	7	188	85	1	86	119	3	122	103	3	106	129	18	147	837	1495
Thysanura	16	2	18	7	2	9	2	—	2	12	—	12	6	3	9	4	1	5	55	91
Orthoptera	1	—	1	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	2	4
Isoptera	1	—	1	—	—	—	—	—	—	4	4	8	—	—	—	—	—	—	9	9
Thysanoptera	1	—	1	1	—	1	1	—	1	2	—	2	2	—	2	6	—	6	13	39
Psocoptera	—	—	—	—	—	—	—	—	—	12	2	14	—	—	—	—	—	—	14	15
Hemiptera (nymphs)	3	1	4	27	1	28	17	—	17	8	1	9	6	1	7	6	1	7	72	96
Hemiptera (adults)	—	1	1	—	—	—	7	—	7	—	—	—	—	—	—	1	—	1	9	9
Hemiptera (Coccids)	3	5	8	29	2	31	9	—	9	8	—	8	21	—	21	1	—	1	78	162
Coleoptera (larvae)	1	1	2	—	—	—	2	5	7	—	1	1	—	2	2	2	—	2	14	37
Coleoptera (adults)	12	1	13	36	1	37	17	5	22	13	3	16	11	2	13	8	1	9	110	161
Diptera (larvae)	5	—	5	4	—	4	1	—	1	2	—	2	11	—	11	—	1	1	24	33
Diptera (adults)	1	1	2	1	—	1	3	1	4	1	1	2	1	1	2	—	—	—	11	22
Lepidoptera (larvae)	1	—	1	4	—	4	—	—	—	—	—	—	—	—	—	—	—	—	5	7
Lepidoptera (adults)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
Hymenoptera (not ants)	—	—	—	—	—	—	1	1	2	1	1	2	—	—	—	—	—	—	4	5
Formicidae (larvae)	—	—	—	—	—	—	48	—	48	—	—	—	—	—	—	—	—	—	48	57
Formicidae (adults)	78	31	109	15	—	15	112	8	120	9	1	10	13	23	36	88	9	97	387	649
Undetermined larvae	—	—	—	—	—	—	1	—	1	—	—	—	1	—	1	—	—	—	2	2
Totals	828	85	913	876	29	905	659	32	691	806	55	861	797	68	865	629	98	727	4962	7655

PHLOEOTHRIPIDAE: *Eurythrips cinctus* Hd., *Eurythrips* sp., *Metriothrips* sp., Hoplothripinae, 1 sp.

The Thripidae were the commonest Thysanoptera present, especially the species of *Frankliniella*, which was feeding on the grass foliage. It should be mentioned that this species is probably not hypogoeic, and its presence in the samples is almost certainly accidental.

Psocoptera. PSOQUILLIDAE: *Psocatropos* sp., undetermined nymphs.

The nymphs formed the bulk of the 15 Psocids in the samples. It is possible that they are the same species of *Psocatropos* as the four adults.

Hemiptera, Heteroptera. LYGAEIDAE: *Valtissus distinctus* Dist. CERATOCOMBIDAE: *Cryptostemma sordida* China.

Hemiptera, Hymenoptera. JASSIDAE: *Thamnotettix colonus* Uhler, and undetermined nymphs. DELPHACIDAE: undetermined nymph. PSEUDOCOCCIDAE: *Morrisonella americana* Hambl., *Rhizoecus* spp.

Only nine adult Hemiptera (apart from the Coccids) were present in the samples, four of these being the Jassid. With the exception of six nymphs of the new species of *Cryptostemma* (being described by Dr China) all of the Hemipterous nymphs were Jassids and Delphacids, the Jassids being commonest. No Ortheziid Coccids were found in the savannah plot.

Coleoptera. HYDROPHILIDAE: ?*Cercyon* sp. STAPHYLINIDAE: *Oxytelus incisus* Motsch, *Neotrochus* sp., *Diochus nanus* Er., *Osorius* sp., *Trogophloeus* sp., *Stenus* sp., *Coprophilus rutila* Er., Paederini, two undetermined species; one other undetermined species. HISTERIDAE: *Hister* sp. SCYDMAENIDAE: *Eucomus* sp., *Scydmaenus* sp. PSELAPHIDAE: *Euplectus* sp., one undetermined species. DRYOPIDAE: one undetermined species. CUCUJIDAE: two undetermined genera. APHODIDAE: one undetermined species. CURCULIONIDAE: one undetermined species. SCOLYTIDAE: two undetermined genera.

In addition to these adult beetles, the following families were represented in the larval state: STAPHYLINIDAE (Staphylininae spp., *Paederus* spp.), PTILIIDAE, HISTERIDAE, CANTHARIDAE (Malthinae, 1 sp.), ELATERIDAE (Pyrophorinae sp.).

The commonest adult beetles were again representatives of the Staphylinoidea, the most abundant species being *Coprophilus rutila*. The next commonest was an indetermined Scolytid, this forming 10% of the total adult beetles collected. The presence of one adult Hydrophilid, an essentially moisture-loving family, in the sample taken on 17 February, as the soil was really drying out, is of some interest, and hard to explain.

Hymenoptera. CYNIPIDAE: *Cothonaspis* sp. FORMICIDAE.

The ant collection, as has already been mentioned, was lost in transit to a specialist, and all that can be said is that a species of the coccidophilic genus *Rhizomyrma* was extremely common on the savannah plot. Ants of the genera *Pheidole* and *Solenopsis* were present in most of the samples.

Diptera, Nematocera. HELEIDAE: *Dasyhelea* spp. CECIDOMYIDAE: undetermined genera.

In addition to adults of these families, larvae of Heleids, other Nematocerous flies, and what was apparently one species of Cyclorrhaphous Anthomyiid were present. The majority of the dipterous adults were small Cecidomyids, and it is surprising that only ten out of the 33 larvae in the samples could be assigned to this family. The majority of the larvae were Anthomyiids, and it is possible that some non-hypogoeic stem-borers were present.

ARACHNIDA.

Araneae. LINYPHIIDAE: *Eperigone* sp., *Microneta* sp. ULOBORIDAE: *Uloborus* sp.

The small number of non-acarine arachnids on the savannah plot is of interest. The commonest spiders were of the species, probably new to science, of *Eperigone*, of which six specimens were taken.

ACARINA.

LAELAPTIDAE: *Cosmolaelaps* sp., *Hypoaspis* sp., *Seiulis* sp. TRACHYUROPODIDAE: *Urojanetia* sp. UROPODIDAE: *Uroplitella* sp.

It is interesting that only five species of Acarines, representing only three families, were present in the samples. Further, that the commonest family, the Laelaptids, did not occur at all in the cacao plot samples.

In the savannah plot, then, *at least* 13 orders, 39 families, and 70 species of arthropods were encountered. This estimate, especially with regard to the species, is probably too low. It must, however, be remembered that twice as many samples were taken on the savannah as on the cacao plot, and therefore a more accurate picture of the population should be available. It is thus possible to state with some certainty that the cacao plot contains a far wider range of species in the litter and first three inches of soil than the savannah plot.

(*b*) *The quantitative results*

The cacao plot. Table 3 gives the quantitative results for the six series of samples taken on the cacao plot. As would be expected, the bulk of the population was made up by the mites (47%), springtails (20%), and ants (17%), which together formed 84% of the animals present. Of the minor groups, the Thysanoptera deserve mention. The sudden increase of thrips (mostly *Frankliniella insularis*) in February, just as the dry season was getting really

intense, and rainfall and humidity were at their lowest, is puzzling, and can only be accounted for by the supposition that the bulk of the population were aerial feeders who had moved down into the litter layer in response to the low atmospheric humidity. This explanation might serve to account also for the larger numbers of adult beetles and non-acarine arachnids found in the litter at this period.

The savannah plots. Tables 4 and 5 give the quantitative results for the six series of samples taken respectively on the whole and subplots. A remarkable point about these tables is that they show the subplot population to be much higher than the whole plot. This is a useful reminder that soil samples should be taken over as wide an area as possible if an accurate picture of the numerical population is to be obtained. The percentages of the major groups occurring on the whole and subplots are given in Table 6 below.

Table 6. *Percentages of major groups in the savannah plots*

	Whole plot	Subplot	Totals
Mites	55	63	59
Springtails	24	18	19
Ants	10	9	9
Others	11	10	13

It will be noted that the major groups are of the same order of magnitude in both the whole and subplots. The mites, even though represented by a far smaller number of families and species, form a greater percentage of the fauna than in the cacao plot. This seems to suggest that they were specialized hypogoeic forms as distinct from litter dwellers. The ants form a correspondingly smaller proportion of the total arthropods present.

5. DISCUSSION

Two facts of some interest are shown by the results detailed in the preceding sections. First, there is a definite downward migration of certain groups of soil animals in response to the decreased rainfall and humidity as the dry season advances. This is particularly true of the Acarina and Collembola. In the cacao plot, for example, 79% of the fauna was taken in the litter layer in November. By the end of February, only 41% of the animals were in this layer, and many of these were of essentially arboreal genera that are not usually found in the litter. The ant population figures for this plot (total adult ants in the litter, 0–1½ and 1½–3 in. layers) show this response well when compared with the soil moisture figures for the 1½ in. layer (see Tables 1 and 3) and it would seem as if the complex of species concerned is only present in large numbers in the top soil and litter when the humidity is above an undetermined minimum.

From Table 4 it can be seen that the savannah whole plot population drops to the order of 50% by the end of February. The 1½–3 in. cores for the whole plot show an initial drop, followed by a rise, during the sampling period, indicating a downward migration of part of the population in response to low humidity. The same applies to the subplot, in which, however, migration downwards does not seem to have taken place to such a marked extent. In Table 7, the 1½–3 in. populations have been expressed as a percentage of the whole for the six series of samples. From it can be seen the relative degree of migration in both the whole and subplots.

Table 7. *Percentage population in 1½–3 in. samples*

Sample ...	1	2	3	4	5	6
Whole plot	12·6	9·4	6·6	12·1	7·7	16·6
Subplot	10·2	3·2	4·8	6·4	7·8	13·4

It would seem, from these figures, that a greater percentage of the population of the subplot remained in the surface layer during the first two months of the dry season, and thus that the tall grass (at the time nearly 2 ft. high) on the subplot exerted a buffering effect on the soil animals. It was only in mid-February, as the dry season was at its height, that migration on the subplot equalled in intensity that on the rest of the plot.

The second fact of some importance is that, although the soil on both plots was the same, the constitution of the fauna was quite different. The cacao plot, from the start, had a richer fauna, with a far greater number of families, genera, and species represented than did the savannah plot. In fact, omitting the ants, only 19 of the identified genera are the same for both plots. This cacao plot species' ascendancy is probably largely due to the litter covering the soil surface, with its attendant saprophagous fauna playing an important part in the formation of humus. Comparing the figures for the 1½ in. samples for the cacao and savannah plots, one is struck by the fact that the populations are remarkably close, especially before the dry season begins to make its presence felt. Yet the two major groups determining the numerical populations of this layer (the ants and mites) differ markedly in composition. It would seem, therefore, that there is a real difference in the generic complexes of the two plots, and this must be ascribed largely to the differing environmental conditions on the plots, which, in turn, are largely a result of the closed, 'protective' canopy on the cacao plot, and the bare, exposed grass on the savannah plots.

6. SUMMARY

Soil samples were taken at approximately fortnightly intervals on two plots, one under the relatively stable climatic conditions of a mature cacao field, the other under the exposed conditions of open savannah land, between November 1943 and March 1944. The samples were treated in Berlese-Tullgren funnels, and qualitative and quantitative estimates of the soil fauna of the plots were made. Two conclusions are reached from an examination of the data obtained. (1) In both plots there is a definite tendency for the soil animals living in the surface layer to migrate downwards in response to the decrease in humidity as the dry season advances. (2) There is a very considerable difference in the qualitative populations present on the two plots, in spite of the soil being the same in both cases. It is suggested that this is largely due to the differing plant associations present on the plots.

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REFERENCES

Hambleton, E. J. (1946). 'Studies of hypogoeic mealybugs.' Rev. Ent. 17: 1–77.

Hoff, C. C. (1945). 'The Pseudoscorpion subfamily Olpiinae.' Amer. Mus. Novit. 1291: 1–30.

Jacot, A. P. (1936). 'Soil structure and soil biology.' Ecology, 17: 359–79.

Posnette, A. F. (1944). 'Pollination of cacao in Trinidad.' Trop. Agriculture, Trin., 21: 115–18.

Strickland, A. H. (1945). 'A survey of the arthropod soil and litter fauna of some forest reserves and cacao estates in Trinidad, British West Indies.' J. Anim. Ecol. 14: 1–11.

Trägårdh, I. (1933). 'Methods of automatic collecting for studying the fauna of the soil.' Bull. Ent. Res. 24: 203–14.

Tullgren, A. (1917). 'En enkel apparat för automatiskt vittjande av sållgods.' Ent. Tidskr. 38: 97–100.

THE GENERIC RELATIONS OF SPECIES IN SMALL ECOLOGICAL COMMUNITIES

By C. B. WILLIAMS, *Rothamsted Experimental Station, Harpenden*

1. INTRODUCTION

The problem of the importance of competition between two or more species in the same genus, in determining whether they can survive side by side in the same community, is of great ecological interest. The following is a statistical approach to the problem based largely on the fact that in most animal and plant communities the numbers of genera with one, two, three, etc., species appear to form a mathematical series very close to the 'logarithmic series'.

The species in any group of animals and plants that are found living side by side in any relatively small community have presumably been selected in the course of time from all the species in the surrounding areas which have been able to reach the smaller area in question. Those that survive are those which are capable of existing in the physical environment of the area and also in association with, or in competition with, the other members of the community.

Such a natural selection could conceivably be brought about under three different conditions: (1) without reference to the generic relations of the species, (2) more or less *against* species in the same genus, (3) more or less *in favour of* species in the same genus. Extremes of either (2) or (3) would result in only one species to each genus on the one hand, or in all the species in each genus on the other hand being represented. We know, however, that biologically, neither of these extremes is correct.

It is, however, most important to consider in detail what exactly happens when a selection of a relatively small number of species is made from a larger fauna or flora, without reference to their generic relations (no. (1) above), as a true interpretation can only be made by comparing the observed data with the results of a selection of the same size made at random. If the average number of species per genus in a small community is smaller than that expected by random sampling, then there is evidence of a selection against generically related species; if the number of species per genus is larger than would be expected by random sampling, then there is evidence of selection in favour of species in the same genus.

Before we can discuss the problem of sampling, it is, however, necessary to consider what is the general structure of the relative numbers of genera with 1, 2, 3, etc., species in any group of animals or plants.

2. GENERIC CLASSIFICATION AND THE LOGARITHMIC SERIES

I have shown recently (Williams, 1944) that in a number of classifications of particular families or orders of plants, insects and other animals, the number of genera with 1, with 2, with 3, etc., species forms a series which can be represented very closely by the logarithmic series.

This will be discussed more fully below, but for the moment it should be noted that if we know the number of species and the number of genera in any group, a logarithmic series of the genera with 1, 2, 3 species (which we will call n_1, n_2, n_3, etc.) can be calculated and this can be checked against the observed frequencies. If a close fit is found, it is evidence of the likelihood that the logarithmic series is a correct interpretation, and we can then use for further argument known properties of the logarithmic series.

I have shown, as stated above, that the logarithmic series gives a very close fit to published classifications of large groups, such as the flowering plants of Britain, the Mantidae of the world, the birds of Great Britain, and many other systematic and geographical groups. It is, however, important to know if the same principle is found in the classification of small communities. For this purpose some evidence brought forward recently by Elton (1946) is of great value.

Table 1 shows particulars of ten of his animal communities and three of his plant communities, together with the total (reduced to an average) of his 49 animal and of his 27 plant communities; with the number of genera with 1, 2 and 3 species in each case as given by Elton and as calculated by the logarithmic series.

The communities analysed here are all comparatively simple ones, because reliable surveys of more complex communities such as woodland do not yet exist; some of them, however, are quite large in area.

No one can deny the extremely close approximation of the observed and calculated figures in nearly all the examples and particularly in the averages. Thus in the average figure for 49 animal communities the calculated number of genera with one

species is 38·1—the observed 39; in the average of 27 plant communities the calculated number of genera with one species is 30·7 and the observed 31·1. The fit for n_2 and n_3 is almost equally good.

Thus we have very strong evidence that the number of genera with 1, with 2 and with 3, etc., species is arranged in a logarithmic series in quite small or simple ecological communities as well as in large systematic groups and in large areas.

where the successive terms are the numbers of groups (in this case genera) with 1, with 2, with 3, etc., units (in this case species).

n_1 (which $= \alpha x$) is the number of genera with one species; x is a constant less than unity, α is a constant which we have called the Index of Diversity. If we know the number of species (N) and the number of genera (S) in a population which is arranged in a log series, we can calculate both n_1 and x, and

Table 1

	Elton's community	No. of genera	No. of species	No. of genera with 1 species	2 species	3 species	Index of diversity
	Animal	S	N	n_1	n_2	n_3	α
9	Temperate woodland (logs)	126	136	118	6	2	
				116	*8·7*	*0·9*	773·
10	Subarctic bog	19	21	17	2	0	
				19·1	*1·6*	*0·2*	94
11	Subarctic bog	29	32	26	3	0	
				26·3	*2·2*	*0·25*	155
12	Temperate fresh-water pond	26	32	21	4	1	
				21·4	*3·5*	*0·8*	65
13	Temperate fresh-water pond	72	90	61	8	1	
				59	*11*	*2·2*	171
14	Temperate lake benthos	46	59	38	6	0	
				36·8	*6·9*	*1·7*	98·1
15	Temperate lake benthos	8	13	6	1	0	
				5	*1·8*	*0·7*	8·3
16	Temperate lake benthos	58	86	44	8	1	
				40	*10·8*	*3·9*	74
20	Temperate river	99	131	82	7	6	
				79·6	*15·6*	*4·1*	203
22	Temperate river	59	87	47	6	3	
				42	*10·8*	*3·7*	81·5
	Average of 49 animal communities	45·3	54·41	39·0	4·6	1·12	
				38·1	*5·7*	*1·14*	127
	Plant						
1	Arctic rocky soil	22	31	16	4	1	
				16·4	*3·9*	*1·2*	35
3	Arctic heath	37	51	28	7	0	
				27·8	*6·3*	*1·9*	62
4	Subarctic heath	32	42	26	3	0	
				26	*4·9*	*1·35*	68
	Average of 27 plant communities	37·0	95·1	31·1	4·4	1	
				30·7	*4·9*	*1·05*	96

Data from Elton (1946). Numbers in col. 1 are those of communities given in his Tables 1 and 4.
In the figures for n_1, n_2 and n_3 the upper line is the observed number, the lower line (in italics) that calculated on the basis of the log series.

3. THE PROPERTIES OF THE LOGARITHMIC SERIES

The logarithmic series will be found fully discussed in Fisher, Corbet & Williams (1943), Williams (1944) and Williams (1947).

The series can be represented in two ways, either

$$n_1, \quad \frac{n_1 x}{2}, \quad \frac{n_1 x^2}{3}, \quad \frac{n_1 x^3}{4},$$

or

$$\alpha x, \quad \alpha\frac{x^2}{2}, \quad \alpha\frac{x^3}{3}, \quad \alpha\frac{x^4}{4},$$

hence the whole series, and also the Index of Diversity.

If a random sample is taken from a population which is arranged in a logarithmic series, a new logarithmic series is found in the sample, with a new n_1 and a new x. But for all samples of whatever size from one population the ratio of n_1 to x, which we have called 'α', is constant. In other words, this is a property of the population and not of one particular sample. It is a measure of the extent to which the species are grouped into genera, or the genera

divided into species. It is high when there are a large number of genera in relation to the number of species, and low when there are a small number of genera relative to the number of species, and it is independent of the size of the sample. It is thus a measure of the generic diversification of the species population, and for this reason we have called it the 'Index of Diversity'. It is, indeed, an index of exactly the property which is at present at issue. If a small sample of a larger population has the same Index of Diversity as the larger population, then it has been selected without reference to the generic relationships of the species. If the smaller sample has a larger Index of Diversity, it is evidence that there has been selection against species in the same genus. If it has a smaller Index of Diversity, it is evidence that there has been selection in favour of species in the same genus.

The average number of species per genus (N/S), the proportion of genera with one species (n_1/S), and the proportion of species in genera with one species (n_1/N) are all dependent on the size of the sample (see Table 2); but the Index of Diversity is the same for all samples from the same population provided that they have been randomized for generic relationships.

It is, however, important to note for the present study that the error of estimation of the Index of Diversity increases rapidly as the sample gets smaller (see Fisher *et al.* 1943, pp. 53 and 56). Thus for populations with 1000 species in 100 genera the error (standard deviation) of α is about 6%; but with 100 species in 70 genera it is 20%, and with 10 species in 9 genera it is just under 100%. The error is particularly high when the average number of species per genus is very low, which is usually the case in small communities.

An example of the application of the logarithmic series is as follows: In Bentham & Hooker's *British Flora*, 1906 edition there are 1251 species of plants classified into 479 genera. These are arranged reasonably closely to a logarithmic series and give an Index of Diversity = 284 (Williams, 1944, p. 30).

If samples of different numbers of species are taken from the above flora, *without any reference to generic relationships*, they must each have the same index of diversity; and from this and the number of species we can calculate that the expected number of genera would be, as shown in Table 2.

Table 2. *Calculated properties of samples of different numbers of species taken from Bentham & Hooker's 'British Flora'* (1906 *ed.*), *without any bias with respect to generic relations. All samples have an Index of Diversity of* 284.

No. of species	Expected no. of genera	Average no. of species per genus	Expected no. of genera with 1 species	% of genera with 1 species
N	S	N/S	n_1	$100\,n_1/S$
		Original population		
1251	479	2·61	231	48
		Samples		
1000	428	2·34	222	52
500	288	1·74	181	63
200	151	1·32	117	78
100	86	1·16	74	86
50	46	1·09	42·5	92
30	28·5	1·05	—	—
20	19·3	1·04	18·7	95
10	9·8	1·02	—	—

It will be seen that the average number of species per genus steadily falls, and the percentage of genera with one species each steadily rises as the sample gets smaller. In a random sample of only 20 species of British flowering plants less than one genus with more than one species would be expected to be present.

It should be noted that if our biologically selected community contains as few as 30 species, the only possible high values for n_1 (since fractions do not exist in nature), are 30; 29; 28; 27; 26; 25. These give respectively Indexes equal to infinity; 420; 270; 195; and 150, etc. so that no community as small as this will give statistical data sufficient to distinguish between small changes in α, or small biases in favour of, or against, species in the same genus.

The data brought forward by Elton are not suitable for further inquiry along these lines as firstly

the numbers of species are in general too small, and secondly we have no available lists of the number of species and genera (and that is to say of the Index of Diversity) in the larger groups, floras or faunas, from which these communities have been selected by nature. What we require is a series of natural groups of different sizes selected by nature from one much larger group; all the species and genera in each series being of course in exactly the same classification.

For example, if we could take the butterflies of the world, the butterflies of England, the butterflies of an English county, the butterflies of a small area in this county, and the butterflies of a single ecological community in the small area (all in the same classification), then we would have a series of observed facts which could be analysed to see if the Index of Diversity in each sample indicated greater or less generic diversification as the samples got smaller.

It has not been possible to get such a perfect series of data, but in what follows I give the evidence I have been able to find that appears to be suitable for study.

The two Broadbalk Communities thus have—as would be expected from the small size of the sample—a lower average number of species per genus; but the Index of Diversity is in each case lower than the whole British flora, and the smaller sample has a lower value than the larger. Thus the evidence is that there is less generic diversification in the Broadbalk Wilderness flora, or a smaller number of genera than would be expected by a random sample including the same number of species.

In fact a random sample of 73 species from the British flora, as classified by Bentham & Hooker, would have about 65 genera instead of the 59 observed.

(*b*) *Flowering plants of Scolthead Island, Norfolk*

Chapman (1934) gives a list of the flowering plants of Scolthead Island, an island of sand-dunes which covers an area of about one and a half square miles.

His list, when altered to the nomenclature of Bentham & Hooker's *British Flora* (1906 ed.), gives the following results (Table 3).

Table 3

Species N	Genera S	Species per genus N/S		No. of genera with 1 species n_1	2 species n_2	3 species n_3	4 species n_4	5 species n_5	Index of Diversity
161	114	1·41	Obs.	82	22	7	1	2	
			Cal.	85·3	20·1	6·3	2·26	0·8	182

4. COMPARISONS OF SMALL WITH LARGE SERIES

(*a*) *Plants on Broadbalk Wilderness, Rothamsted Experimental Station, Hertfordshire*

Brenchley and Adam (1915) have published a list of the species of flowering plants that have been found on this piece of abandoned wheat field which covers an area of about half an acre. In their table on p. 198 (emended to agree with the nomenclature of Bentham & Hooker's *British Flora*, 1906 ed.), they mention 73 species which were found in four surveys carried out between 1867 and 1913. These are classified into 59 genera. Of these, 50 genera have one species; six have two species; one has three and one has four. This gives an average number of species per genus of 1·24; and an Index of Diversity of 147.

If only the plants observed in 1913 are considered, the numbers are 65 species in 52 genera (41 with one species, ten with two, one with three). The average number of species per genus is 1·25 and the Index of Diversity 134.

I have already published (Williams, 1944, p. 30) data on the whole classification of Bentham & Hooker's 1906 edition which gives an average number of species per genus of 2·61 and an Index of Diversity = 284.

It will be seen that the observed numbers conform very closely to a logarithmic series as checked by the calculated values of n_1, n_2, and n_3; and that the Index of Diversity is 182, as compared with 284 for the whole British flora.

In a purely random sample of 161 species from the British flora, irrespective of generic relations, we would have expected to find representatives of approximately 126 genera. Thus the observed number is smaller than the calculated, indicating a selection in favour of generically related species rather than against them.

(*c*) *Flora of Park Grass Plots, Rothamstead Experimental Station, Hertfordshire*

At Rothamsted there are a series of plots of grass, of areas varying from $\frac{1}{2}$ to $\frac{1}{8}$ acre, which have been manured in special ways for many years, but in which no further interference has been made in the natural flora which develops under such conditions of manuring and soil.

Brenchley (1924) has given a series of tables from which Table 4 is extracted; the classification has been altered slightly to agree with Bentham & Hooker's *British Flora* (1906 ed.).

Table 4

	No. of species N	No. of genera S	Average species per genus N/S	Index of Diversity
All plots all years	59	53	1·11	263
1919 Survey only				
Plot 3. Unmanured:				
Without lime	30	27	1·11	134
With lime	30	27	1·11	134
Plot 13. Farmyard manure:				
Without lime	20	18	1·11	89
With lime	23	21	1·10	111

The original Index of Diversity for the whole of Bentham & Hooker was 284 so that all the smaller floras have a smaller Index of Diversity. The error of estimation of α is however very high.

Plots 9 and 10, with sulphate of ammonia for many years, gave (with and without potash) from 9 to 14 species each in its own genus. It is not possible to calculate a finite value of α from such data. It is, however, interesting to note that in a random sample of ten species from Bentham & Hooker's *British Flora* ($\alpha = 284$) one would expect 9·8 genera! So the observed figure of 10 cannot be taken as evidence of any extreme departure from randomization.

(*d*) *Lepidoptera of Wicken Fen, Cambridgeshire*

Farren (1936) gives a list of the Macrolepidoptera of Wicken Fen according to the classification of Meyrick's *Handbook of the British Lepidoptera* (1895). In the whole group 368 species are listed in 135 genera. This gives an average of 2·73 species per genus and an Index of Diversity of 76·4. The number of species in the same families for the whole of Great Britain, as listed in Meyrick's handbook, is 788 in 212 genera, which gives an average of 3·72 species per genus and an Index of Diversity of 96·5.

For the family Caradrinidae (Agrotidae) alone, there are 146 species in 29 genera for Wicken Fen (average per genus 5·04; Index of Diversity 10·8); and 273 species in 39 genera for the whole of Great Britain (average per genus 7·00; Index of Diversity 12·7). In the family Plusiidae there are 24 species in 12 genera for Wicken Fen (average 2·00; $\alpha = 9·3$) and 54 species in 22 genera for the British Isles (average 2·45, $\alpha = 14·0$).

So we see that for the whole Macrolepidoptera and also for two separate families, one large and one small, the Index of Diversity of the local fauna is smaller than that of the larger area. In other words, there are fewer genera in the local fauna than would be expected by a random selection, thus giving evidence of a selection in favour of generically related species.

(*e*) *Coleoptera of Windsor Forest, Berkshire*

Donisthorpe (1939) gives a list of 1825 species of Coleoptera found in Windsor Forest. They are grouped into 553 genera, according to the classification of Beare & Donisthorpe (1904). The list gives a good approximation to a logarithmic series. There is an average of 3·30 species per genus and an Index of Diversity of 278. The original classification of the Coleoptera of the British Isles gave 3268 species in 804 genera, with an average of 4·60 species per genus and an Index of Diversity of 341 (see Williams, 1944, p. 24). Thus the Coleoptera of Windsor Forest have, as expected from the smaller number of species, a lower average number of species per genus; but have also a smaller Index of Diversity, indicating a selection in favour of species of the same genus rather than against.

(*f*) *Capsidae* (= *Miridae*) (*Heteroptera*) *of Hertfordshire*

China (1943) gives a list of the Heteroptera of the British Isles. The family Capsidae (= Miridae) in this includes 186 species in 76 genera as shown in Table 5. The Index of Diversity is 48.

Table 5

No. of species N	No. of genera S	Average sp. per gen. N/S		No. of genera with 1 species n_1	2 species n_2	3 species n_3	4 species n_4	5 species n_5	Index of Diversity
			British						
186	76	2·45	Obs.	40	16	11	3	1	
			Cal.	38·1	15·2	8	4·8	—	48
			Hertfordshire						
127	60	2·12	Obs.	39	12	3	1	0	
			Cal.	32·5	12·1	6	—	—	43·7

Bedwell (1945) has given a list of the Hemiptera of Hertfordshire; the particulars of the Capsidae from this are given in the second half of Table 5. It will be seen that the Index of Diversity is slightly below that of the British fauna, but probably not outside the limits of error.

It shows, however, no evidence of selection against species of the same genus.

180 species in 33 genera in Hertfordshire (average 5·15, $\alpha = 13{\cdot}2$), and 290 species in 45 genera for the British Isles (average 6·44; $\alpha = 14{\cdot}9$). Thus the differences indicated that the smaller faunas have an Index of Diversity just equal to or smaller than the larger areas.

It is interesting to note that Meyrick wrote his first *Handbook* in 1895, and his 'Revised' edition in

Table 6

Plants	No. of species observed	No. of genera obs.	No. of genera calc.	Av. no. of species per genus obs.	Av. no. of species per genus calc.	Index of Diversity orig.	Index of Diversity sample
Broadbalk: 4 surveys	73	59	65·0	1·24	1·12	284	147
1913 survey	65	52	58·5	1·25	1·11	284	1·34
Scolthead Island	161	114	126	141	1·28	284	182
Park Grass, all plots	59	53	55·9	1·11	1·055	284	263
Plot 3 (1919)	30	27	28·5	1·11	1·05	284	134
Plot 13 (1919)	20	18	19·3	1·11	1·04	284	89
Plot 13 (1919)	23	21	22·2	1·10	1·04	284	111
Insects							
Wicken Fen:							
Macrolepidoptera	368	135	151·6	2·73	2·43	96·5	76·4
Caradrinidae	146	29	32·1	5·04	4·55	12·7	10·8
Plusiidae	24	12	14·0	2·00	1·71	14·0	9·3
Windsor Forest:							
Coleoptera	1825	553	630·0	3·30	2·90	341·0	278
Hertfordshire:							
Miridae	127	60	62·1	2·12	2·05	48	43·7
Macrolepidoptera	561	186	188·4	3·02	2·98	99·6	99
Caradrinidae	180	33	38·31	5·15	4·70	14·9	13·2

Table 7

No. of species in sample	No. of genera in sample 1	2	3	Av. no. of genera in sample	Observed no. in natural samples of same
20	20	19	20	19·7	18
23	23	22	22	22·3	21
30	29	28	29	28·7	27
59	56	50	54	53·3	53
65	60	54	59	59·7	52
73	67	60	66	64·3	59
161	128	117	126	123·7	114

(g) *Lepidoptera of Hertfordshire*

Foster (1937) gives a list of the Lepidoptera recorded for Hertfordshire. The classification used is that of Meyrick's, *Revised handbook of British Lepidoptera* (1927). He enumerates 561 species in 186 genera. This gives an average of 3·02 species per genus and an Index of Diversity of about 99. In Meyrick's *Revised handbook* the figures for the same families for the whole British Isles are 806 species in 218 genera. This is an average of 3·7 species per genus and an Index of Diversity of 99·6. In the Family Caradrinidae (Agrotidae) alone, there are

1927. The first gives an Index of Diversity of 96·5, the second of 99·6; which shows how little his ideas on the scope of genera had changed in the 32 years between the two editions.

5. DISCUSSION

In Table 6 is a summary of the evidence brought forward in seven plant communities and seven animal communities. None of them is very small, as we have already explained that in the very small communities the chance of getting two species in one genus is too low to be the basis of discussion.

The table shows the number of genera observed in each natural sample and also the number of genera calculated on the assumption that it is a random sample from a larger flora or fauna which is arranged in a logarithmic series. It will be seen that in practically every case the observed number of genera is smaller than the calculated. It follows that the observed average number of species per genus is larger than that calculated on the assumption of a random selection from a logarithmic series, although much smaller than that in the larger area used for comparison.

These figures are calculated on the acceptance of the logarithmic series. If this is not accepted, it is still possible to make a practical demonstration that the same difference still exists between observed figures and a random sample. Bentham & Hooker's *British Flora* contains 1251 species. A series of numbers up to 1251 was typed on small cards and extremely well mixed. Three complete sets of random samples were then drawn from the complete set, each set being returned before the next set was selected. At intervals during the draw the number of genera represented in the species already selected was checked up. The results were as shown in Table 7. It will be seen again that in every case except one the observed natural number of genera is smaller than any of the three sets of mechanically randomized samples taken from the original flora. The amount of data at present available is insufficient for an overwhelming proof that the number of genera is really smaller, but at least it contains no evidence whatever that the number of genera is larger in a natural sample than in one selected absolutely independent of generic relationship, which would be expected if competition between species of the same genus was a major factor in determining survival.

From all this evidence it will be seen that a statistical treatment of the number of genera and species of different groups of animals or plants, in small and in large communities, indicates that the 'diversification' of species into genera is smaller in the small samples than in the larger. In other words, the smaller samples have fewer genera than would be expected in a random sample of the same number of species taken from the larger fauna or flora. This can only be interpreted as a natural selection—in the course of time—in favour of species in the same genus rather than against them.

It is possible to suggest reasons for this—for example, if one species in a genus is capable of survival in a given physical environment, it seems likely that other species in the same genus might be more likely to have a similar genetic make-up than species in another genus, and so might also have a good chance of survival.

If two or more species in the same genus are each capable of surviving in a particular ecological niche, the problem of their joint survival seems to be a question of the balance between the advantages of suitability to the physical environment and the disadvantages of the increased number of competitors with very similar habits—not only individuals of the same species, but of other species very closely related.

There are undoubtedly increasing difficulties to a species when the numbers increase beyond a certain level and in some cases the individuals of two closely related species might act almost as individuals of the same species, and so bring all the difficulties of increased numbers (e.g. competition for available food) without any compensating advantages.

The evidence at our disposal, however, seems to indicate that on an average, the advantages of increased suitability to the environment outweighs the disadvantages of any possible intensification of competition due to close relationship. Such increased competition possibly, or even probably, exists, but its effect cannot be estimated by study of the present type, as it is undoubtedly overshadowed by other factors acting in a reverse direction.

6. SUMMARY

1. Evidence of conditions being more favourable or less favourable to species of the same genus, as compared with species on different genera (intra-generic versus inter-generic competition), can be found in the relative number of species and genera in small and in large natural communities of animals or plants.

2. It is, however, insufficient to show that the average number of species per genus is smaller in the smaller communities than in the larger as this is a mathematical result of taking a smaller sample from a larger group. It is necessary to show that the proportion of genera to species in the smaller communities is *smaller* or *larger* than would have been expected in a randomized sample of the same number of species, selected without reference to generic relationships from the larger fauna or flora.

3. Evidence had previously been brought forward to show that in large groups of animals or plants the number of genera with 1, 2, and with 3 and more species are closely represented by the mathematical 'logarithmic series'. New evidence is here given to show that the same order exists in the genera and species of quite small ecological communities.

4. The logarithmic series has several mathematical properties of biological interest, including the possibility of calculating, for any population or sample, a factor known as the 'Index of Diversity' which is common to all random samples from a single population. It is a measure of the extent to which the species are grouped into genera, and it is inde-

pendent of the size of the sample. If the Index of Diversity is high, there are many genera in relation to the number of species; if the Index is low, there are fewer genera in relation to the number of species.

5. It thus becomes possible to compare the Index of Diversity in natural small or simple ecological communities, with that of the larger population from which these have been selected by nature. This has been done for a number of cases, including both animal and plant communities, and in every case from which significant results can be obtained the Index of Diversity in the small community is smaller than that of the larger fauna or flora.

6. The result therefore indicates that there are fewer genera in a small or simple community than would be expected in a sample of the same number of species selected at random—that is, independent of genera relationships—from the larger series. In other words, the evidence brought forward by this method indicates a selection by nature in favour of more than one species in the same genus rather than in favour of single species in different genera.

REFERENCES

Beare, T. H. & Donisthorpe, H. St J. K. (1904). 'Catalogue of British Coleoptera.' London.

Bedwell, E. C. (1945). 'The county distribution of the British Hemiptera-Heteroptera.' Ent. Mon. Mag. 81: 253–73.

Brenchley, W. E. (1924). 'Manuring of grass land for hay.' London.

Brenchley, W. E. & Adam, H. (1915). 'Recolonisation of cultivated land allowed to revert to natural conditions.' J. Ecol. 3: 193–210.

Chapman, V. J. (1934). 'Appendix II. Floral list.' In J. A. Steers 'Scolthead Island....' Cambridge. Pp. 229–34.

China, W. E. (1943). 'The generic names of the British Hemiptera-Heteroptera, with a check list of the British species.' In 'The generic names of British Insects,' Part 8: 217–316. London: R. Ent. Soc.

Donisthorpe, H. St J. K. (1939). 'A preliminary list of the Coleoptera of Windsor Forest.' London.

Elton, C. (1946). 'Competition and the structure of ecological communities.' J. Anim. Ecol. 15: 54–68.

Farren, W. (1936). 'A list of Lepidoptera of Wicken and the neighbouring Fens.' In J. S. Gardener, 'The natural history of Wicken Fen', Part III: 258–66. Cambridge.

Fisher, R. A., Corbet, A. S. & Williams, C. B. (1943). 'The relation between the number of species and the number of individuals in a random sample of an animal population.' J. Anim. Ecol. 12: 42–58.

Foster, A. H. (1937). 'A list of the Lepidoptera of Hertfordshire.' Trans. Herts. Nat. Hist. Soc. 20: 171–279.

Williams, C. B. (1944). 'Some applications of the logarithmic series and the Index of Diversity to ecological problems.' J. Ecol. 32: 1–44.

Williams, C. B. (1947). 'The logarithmic series and its application to biological problems.' J. Ecol. 34: 253–72.

THE SIGNIFICANCE OF CLUTCH-SIZE IN THE PARTRIDGE (*PERDIX PERDIX*)

By DAVID LACK, *Edward Grey Institute of Field Ornithology, Oxford*

1. SOURCE OF DATA

This paper on *Perdix perdix* (L.) is one of a series on clutch-size in birds (see Lack (1947) for review and other references). The basic data, which are in the Bureau of Animal Population, Oxford, were collected by A. D. Middleton with the help of gamekeepers and estate managers, and have already been published in summary (Middleton, 1935, 1936*a*, *b*). The records here analysed further are from estates B2, H5, L8, M1 and S1. On these estates, and on C1, every clutch found was recorded. However, the records from C1 were here excluded, because not only was the average clutch-size abnormally high, but the form of the records strongly suggested that some of the keepers had not distinguished between natural clutches and those artificially augmented. The records from most other estates were also excluded, because they were based on selected samples of about 20 nests per year and not on all nests found, hence are possibly biased, a fact to be kept in mind when interpreting Middleton's data.

The present analysis is concerned primarily with first layings. At estates B2, L8 and M1, where clutches were dated, those hatching after 30 June were excluded as probably being repeat layings. At H5, clutches were not dated, but care was taken by the keepers and by Middleton to record only first layings. At S1, clutches were again undated, and a very few repeat layings were almost certainly included among the rest, but the error from this source is thought to have been very small.

I am greatly indebted to the Bureau of Animal Population for giving me access to the data, and to Mr A. D. Middleton for his most helpful interpretative comments and his criticisms of this paper.

2. CLUTCH-SIZE IN ENGLAND

The average of 4051 first layings of the English partridge works out at 14·6 eggs, the commoner clutch-sizes being distributed as shown in Table 1 (see Appendix 1 for full details). Too few dated clutches were available to test whether the size of first layings varies with the date, but this seems not to be the case. The partridge is normally single-brooded, but lays again if the first clutch is destroyed. Repeat layings are smaller than first layings. Thus Middleton (1936*a*) found that 17 repeat layings had an average size of 9·9 eggs, about two-thirds of the average size of a first laying. Repeat layings perhaps tend to be smaller later in the season, but further information is needed to prove this.

Table 1. *Size of first layings of partridge in England*

9 eggs 1%	13 eggs 11%	17 eggs 9%
10 ,, 3%	14 ,, 17%	18 ,, 6%
11 ,, 4%	15 ,, 18%	19 ,, 2%
12 ,, 11%	16 ,, 16%	20 ,, 1%

There are marked annual differences in the average size of first layings, as set out in Table 2. In 4 years at S1, the average varied between 13·3 and 15·4 eggs, while of the fourteen figures available for four estates, the lowest average was 13·2 and the highest 16·2 eggs. The standard deviation for all clutches is 2·3, and, using this figure, all the larger differences in Table 2 are significant.

The factors concerned in these annual differences are not known. They are evidently local because, although the four estates are within a rectangle only 180 miles from north to south and 70 miles from east to west, the variations are not similar at each. For instance, in 1935 clutch-size was average at H5, well above average at L8, and well below average at S1. This suggests that differences in weather are not primarily responsible, unless very local ones. Another suggestion, that clutch-size varies with the density of the population, also seems unlikely to be a major factor. The number of nests found on each estate reflects the partridge density in the year in question. This index, given on the right-hand side of Table 2, does not vary similarly to the average clutch-size. For example, average clutch-size was lowest in 1935 at S1 and in 1937 at H5. In the former case partridges were very abundant, and in the latter case unusually scarce. It has been shown (Lack, 1947) that, in several species, birds in their first breeding year lay, on the average, slightly smaller clutches than older individuals. Hence differences in the age-distribution of the populations might account for some of the differences shown in Table 2, but it seems unlikely that they are responsible for the whole of the differences. This problem therefore requires further study.

3. CLUTCH-SIZE IN OTHER REGIONS

As discussed elsewhere (Lack, 1947), many, though not all, European birds show an increase in average clutch-size from south to north and also from the west to the centre of Europe. In Table 3 are summarized the available data on the clutch-size of the partridge in other regions. The data are few, chiefly because clutch-size is usually given only between limits so wide as to be valueless for comparative purposes. For instance, the standard work on British birds gives the clutch-size as usually 9–20 (Jourdain, 1941).

4. CLUTCH-SIZE IN OTHER GALLINACEOUS SPECIES

The south-north increase in average clutch-size found in the partridge also occurs in some other gallinaceous birds. Thus the quail (*Coturnix coturnix*) has a usual clutch of 6–7 in equatorial and South Africa (Moreau, 1944), of 6–8 in India (Baker, 1935), of 7–9 in the Canary Islands (Bannermann, unpubl.), of 7–12 in England (Jourdain, 1941), and of 8–12 in Norway (Collett, 1921). The ptarmigan (*Lagopus mutus*) has an average clutch of 6·6 eggs in Scotland; but of 8·6 eggs in Finland (data in Lack, 1947). The red grouse (*Lagopus scoticus*) has a clutch of 6–11 eggs

Table 2. *Annual differences in size of first layings*

	Average clutch-size						No. of nests found					
Estate	1931	1933	1934	1935	1936	1937	1931	1933	1934	1935	1936	1937
B2 Yorkshire	—	14·6	15·5	14·6	14·4	14·1	—	61	43	50	45	46
H5 Norfolk	—	—	—	14·3	14·4	13·2	—	—	—	119	335	67
L8 Berkshire	—	—	14·6	16·2	—	—	—	—	103	88	—	—
S1 Cambridgeshire	15·4	14·9	14·9	13·3	—	—	688	543	846	921	—	—

Standard deviation for all clutches: 2·3. For full data, see Appendix 1.

Table 3. *Regional variations in clutch-size*

Region	Average size: 1st layings	Average size: late layings	Source
Finland	17·6	?	Merikallio (1931), 83 clutches
Norway	16–18	?	Collett (1921), general statement
Central Germany	16–20	11–13	Rey (1912), general statement, probably for Leipzig-Halle region
Eastern Galicia (Lwow-Tarnopol region)	15–20	?	Prazak (1898), general statement
Belgium	14–16	?	de Havre (1928), general statement
England	14·6	9·9	This paper, based on Middleton
U.S.A. (Great Lakes)	16·9	9·3	Yeatter (1934), 33 June and July clutches, 8 August clutches
U.S.A. (Washington)	17·1	?	Yocom (1943), 44 clutches

From Table 3 it may be concluded that the partridge shows the same regional trends in average clutch-size as most other European birds. Clutch-size increases from south to north, e.g. it is 14·6 eggs in England but 17·6 in Finland and 16–18 in Norway. Clutch-size also increases from the west to the centre of Europe, e.g. it is 14·6 in England and 14–16 in Belgium, but 16–20 or 15–20 in central Germany and in eastern Galicia, which are at about the same latitude as England, but much farther east. It may be added that the 'Hungarian' partridge introduced to the United States there has an average clutch-size similar to that in eastern Europe, from which region the American birds were taken.

Table 3 also shows that, in Germany and U.S.A., as in England, repeat layings tend to be smaller than first layings.

in Britain (Jourdain, 1941), while the willow grouse (*Lagopus lagopus*), which is a well-marked geographical form of the red grouse, usually lays 9–11 eggs in Finland (Merikallio, 1931).

The west-east trend of increasing clutch-size in Europe is also found in other gallinaceous birds. Thus, in Switzerland the ptarmigan usually lays 8–10 eggs as compared with an average of 6·6 in Britain, the quail lays 8–18 eggs as compared with 7–12 in Britain, and the capercaillie (*Tetrao urogallus*) 6–10 eggs as compared with 5–8 in Britain (Fatio, 1904; Jourdain, 1941).

For various other gallinaceous birds, the clutches as published appear to be similar in Britain, Scandinavia and Switzerland, but often clutch-size is given only between wide limits, and in all cases proper statistical data are badly needed.

The marked decline in clutch-size in repeat layings, found in the partridge, also occurs in the pheasant (*Phasianus colchicus*) (Errington & Hamerstrom, 1937), in the prairie chicken (*Tympanuchus cupido*) (Hamerstrom, 1939) and in the bobwhite (*Colinus virginianus*) (Leopold, 1933, quoting Errington) (see also Lack, 1947, Appendix V).

To conclude, while the data for most other species of gallinaceous birds are sparse, they indicate that the main trends of clutch-size variation found in the partridge also hold for other species in the families Phasianidae and Tetraonidae.

5. EGG-PRODUCTION AND CLUTCH-LIMITATION

The partridge belongs to the category of 'indeterminate' layers, i.e. the size of the clutch is not predetermined in the ovary, but, if the eggs are taken as laid, the partridge lays additional eggs (which would not otherwise have been laid) until the clutch is made up to the normal number. Middleton (private communication) took the eggs as laid from several captive hen partridges, and in this way induced birds to lay up to 50 and 51 eggs in a season. McAtee (1930) has recorded a figure of 52 eggs, and Moser (1932) obtained as many as 77 fertile eggs in a season from one 'Hungarian' hen.

These results show that the normal clutch of the partridge does not represent the potential limit of egg-production, or indeed anything near it, a conclusion which also applies to most other birds (Lack, 1947). Clutch-size and egg-production have not always been distinguished by those discussing the problem, and a false parallel has sometimes been made between the factors influencing the egg-production of a domestic fowl (where the eggs are taken as laid) and the clutch-limitation of a wild bird. Nutrition, for instance, perhaps affects egg-production, but it probably has no important *direct* effect on clutch-limitation in wild birds, except under very special circumstances (Lack, 1947).

In the partridge, the laying of additional eggs evidently depends mainly on the number of eggs present in the nest, but whether this response is evoked by visual or tactile stimuli is not known. Nothing further is known of the mechanism of clutch-termination, and the rest of this paper is concerned with the evolutionary significance of clutch-size. The postulate is made that, though clutch-size is subject to phenotypic variations, it has a hereditary basis, and that the limit at which laying stops is ultimately determined by natural selection. Why, then, should the usual limit in England be 14 or 15 eggs, when the partridge is obviously capable of laying many more?

It has sometimes been stated that clutch-size is adjusted to the mortality of the species so as to prevent over-population. This, however, is fallacious, as discussed elsewhere (Lack, 1947). It is here assumed that clutch-size is selected *per se*. As clutch-size so directly affects the potential number of offspring, selection must be stringent. Clearly, it is the upper rather than the lower limit which requires discussion. Other things being equal, those individuals which lay more eggs will obviously have more descendants than those which lay fewer eggs, unless there is some countering disadvantage in having too large a clutch. This upper limit might be set by (*a*) the weakening effect on the parent of laying too many eggs, (*b*) the number of eggs that the sitting hen can effectively incubate, (*c*) the number of young that the parents can raise. Of these three alternatives, the first can safely be ruled out, since clutch-size is so far below the potential limit of egg-production.

6. HATCHING SUCCESS

The most plausible suggestion is that a hen English partridge is of such a size that it can effectively cover only 14 or 15 eggs, and that, when more are present, some fail to develop owing to inadequate incubation. This view is supported by the practice of certain game managers. Under the 'Euston system', the sitting hen partridge is supplied with dummy eggs, while her own clutch is removed and hatched more safely, either under a domestic fowl or in an incubator. The eggs are returned to the partridge when they are chipping, so that she may raise the brood. Now, on some estates, the number of chipped eggs given to each hen partridge for a brood is 20–25, i.e. greatly in excess of the normal clutch. The latter practice is sensible if the natural limit of clutch-size is determined by the number of eggs which the hen can safely incubate, but is useless or even harmful if this limit is ultimately set by the number of chicks which she can raise. The testing of this point is therefore of practical as well as theoretical importance.

Obviously there is an upper limit to the number of eggs which the sitting hen can properly cover, but what matters is whether this limit is normally reached in nature. Middleton's data include the number of young hatching per nest, so that a test can be made of whether large clutches hatch less well than small ones.

The hatching success of the partridge is about 90% for those nests in which at least one egg hatched, i.e. omitting complete failures (which are mainly lost to predators). Table 4 shows convincingly that the hatching percentage is not at all influenced by the size of the clutch, for clutches of between 8 and at least 20 eggs.

Hence clutch-size is not effectively selected through the number of eggs which the sitting bird can cover.

Table 4. *Hatching success according to clutch-size*

Clutch-size	Total no. of eggs	Percentage hatched	Average no. of young hatched per nest
8	120	90·8	7·3
9	351	88·0	7·9
10	1,080	91·4	9·1
11	1,716	90·6	10·0
12	5,340	90·4	10·8
13	5,681	90·3	11·7
14	9,324	90·2	12·6
15	10,650	90·8	13·6
16	9,552	90·6	14·5
17	6,052	90·3	15·3
18	4,104	90·4	16·3
19	1,520	90·9	17·3
20	840	90·6	18·1
21–29	831	92·1	20·1
4–29	57,202	90·4	13·2

Notes. (1) The above includes all recorded clutches in which at least one egg hatched. Clutches destroyed by predators, in which no eggs hatched, were omitted.

(2) A small number of repeat layings were included in the above analysis. Hence the average clutch-size is slightly smaller than the figure for first layings in Table 1. Such inclusions are legitimate as hatching success, not clutch-size, is being tested in Table 4.

(3) There are quite marked differences in the average hatching success in different years, as set out in Appendix 3. These average differences apply to clutches of every size.

Another theoretical possibility is selection through predation during the laying period. The hen does not incubate until the clutch is complete. One egg is usually laid each day, hence during laying a large clutch is left untenanted for a longer period than a small one, to the extent of a further day for each additional egg. For predation to reduce average clutch-size from, say, 16 to 15 eggs, it would be necessary for slightly more than one in every sixteen nests to be destroyed on the last day of laying. There is no reason to think that predation reaches so high a figure. Moreover, predation of this type could scarcely be responsible for the larger average clutch-size in Finland and Germany than in England, as predators are almost certainly much scarcer in England than in these other countries, owing to the intensive game preservation here. Hence the possible effect of predation during laying can almost certainly be excluded. Once laying is completed, the hen sits closely, and there is no reason to think that large clutches would suffer greater predation than small ones.

7. THE CHICK STAGE

The conclusion seems inescapable that the disadvantage of a large clutch occurs after hatching. With a clutch of 20 eggs about 18 chicks hatch, whereas with a clutch of 14–15 eggs only about 13 chicks hatch. Nevertheless, clutches of 14 and 15 eggs are much commoner than those with 20 eggs, hence broods of 13 young presumably give rise to more adult birds than do broods of 18 young, despite the initial numerical advantage of the latter. I therefore conclude that, with too large a brood, there is a disproportionately high mortality among the young. It is reasonable to suppose that this occurs during, or as a result of, the period during which the young are dependent on their parents, and not later.

Three reasons might be suggested for a disproportionately high mortality in large broods: (*a*) the parents brood the chicks during rain and at night; 13 chicks might be the average maximum that the parents can safely cover; (*b*) large broods might be more conspicuous to predators than small broods, and so attract disproportionate attention from predators, helped by the fact that the young might straggle more in large broods; (*c*) the parents might not be able to find sufficient food for more than a certain number of young.

As already noted, the partridge has on the average a smaller clutch in England than in either northern or eastern Europe. Presumably, natural selection favours a higher brood-size in the latter regions than the former. This suggests that brood-size is not limited either by the brooding capacity of the parents, which could scarcely vary regionally, or by conspicuousness to predators, as predators seem much commoner in northern and eastern Europe than in England. On the other hand, the availability of food might well vary regionally. Further, the late layings of the partridge are smaller than first layings, which suggests that natural selection favours a smaller brood late than early in the summer. This again suggests that brood-size is not limited either by brooding behaviour or by conspicuousness to predators, but the availability of food for the young might well be reduced late in the season.

The south-north and west-east trends of increasing clutch-size, also the decrease after midsummer, occur not only in the partridge and other gallinaceous birds, but also in most European passerine and other nidicolous species (Lack, 1947). In passerine birds, the evidence is now extremely strong that brood-size, and thereby clutch-size, is limited primarily by the amount of food which the parents can bring to the nest per day. The arguments for this, being set out fully elsewhere (Lack, 1947), are not given here. However, owing to the parallel variations found in the partridge, it is relevant to

repeat here that both clutch-size and day-length increase with increasing latitude in summer, and decrease with the season after midsummer, and that with a longer day the parents have longer in which to collect food per day, and so may be able to raise a larger brood at one time.

Nidicolous young are fed in the nest by their parents, so it is readily seen why a larger brood may mean less food for each nestling, and hence why brood-size could be limited by food. The situation is less easy to appraise in a nidifugous species such as the partridge, as the young leave the nest after hatching, and they are not fed by their parents but pick up food for themselves. However, the parents bring the young to food, find it for them, and often make it more readily accessible, e.g. by scratching up the ground, and in particular by opening up ants' nests. It therefore seems not unreasonable to suppose that there is an upper limit, set by food, to the number of young which parent partridges can raise, and that this is the ultimate factor which controls clutch-size. This does not necessarily mean that food shortage acts directly, through starvation. The chicks may starve at times, but weakness from inadequate food would also increase their liability to loss through straggling, through cold or wet, through predator attack and through disease. All that theory requires is that, under English conditions, the young in broods of more than 15 individuals should be rather weaker than the young of slightly smaller broods, so that on the average the latter produce more survivors than the former.

The clutch-size of the partridge is not constant. In England, for instance, first layings vary regularly between 10 and 20 eggs, and more extreme values occur occasionally. Some of these variations are probably phenotypic, but it seems likely that others may have a hereditary basis, hence, if clutch-size is determined by natural selection, the latter evidently works to a rather different figure on different occasions. This is only to be expected if clutch-size is selected through the availability of food for the chicks, as the food supply varies somewhat from year to year, and day to day, according to the weather and other factors. Similar considerations apply to many other birds (Lack, 1947). Clutch-size may be regarded as a type of balanced polymorphism (Ford, 1940). However, it differs from other types in that the frequencies of each class lie on a roughly normal curve, and the only reason that the variation is discontinuous and not continuous is the impracticability of laying fractions of an egg. In the partridge, with a clutch varying from 10 to 20 eggs, the roughly normal nature of the distribution is readily seen. It is far less obvious, but fundamentally the same, in a species like the roseate tern (*Sterna dougallii*), which lays either one egg or two, not more, and here the resemblance to true polymorphism is more apparent.

The view advanced here that the clutch-size of the partridge is limited by the selection of brood-size is capable of proof, though the observations may be hard to undertake in practice. What is required is to capture and mark young partridges from broods of different sizes, and then to determine the number of each type recovered in the winter shooting. Supposing that, through use of the Euston system, half of the hen partridges on a particular estate are supplied with broods consisting of 13 young, and the other half with broods of 20 young. Then, if there is no selection of brood-size, the proportion of each type found in the winter shoots will be 13:20. On the other hand, should the views advanced here be correct, the individuals in the former group will survive proportionately rather better than those in the latter. The extent of the difference will depend, among other things, on the extent to which clutch-size variations are genotypic, and this point ought also to be studied. Owing to the probability of annual variations in the available food supply, the above experiment should be carried out for at least two seasons. In song-birds, a parallel experiment has already been carried out accidentally by bird ringers, and is to be described elsewhere. Should such an experiment on partridges conform with the views advanced in this paper, then the system of artificially augmenting partridge broods to 20 young or more ought to be discontinued as economically unsound, unless it is accompanied by the artificial provision of food for the young.

8. SUMMARY

1. The first laying of the partridge (*Perdix perdix*) in England varies from 10 to 20 eggs, averaging 14·6. Late layings are smaller.

2. There are annual differences in the average size of first layings.

3. Average clutch-size is greater in northern and eastern Europe than in England.

4. Clutch-size is not limited by potential egg-production.

5. Hatching success is equal in clutches of between 8 and at least 20 eggs.

6. Clutch-size is considered to be selected through the food available for the brood and a method of proving this is suggested.

APPENDIX 1

Clutches of Perdix perdix *in England*

No. of clutches of each size

Size of clutch	B2 Yorks					H5 Norfolk			L8 Berks		M1 Northumb					S1 Cambs				Total
	1933	1934	1935	1936	1937	1935	1936	1937	1934	1935	1933	1934	1935	1936	1937	1931	1933	1934	1935	
4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2
7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2
8	.	.	.	.	.	1	2	1	.	.	.	.	.	.	.	2	.	.	8	14
9	1	.	.	.	1	2	4	3	2	1	1	.	.	.	.	6	2	5	15	43
10	1	1	1	.	2	1	13	5	6	2	2	.	3	.	1	8	10	11	42	109
11	1	.	1	1	1	15	22	7	1	1	.	.	.	.	1	17	9	23	54	154
12	7	1	5	7	8	12	41	8	10	1	1	.	2	.	1	50	53	87	160	454
13	3	.	5	6	3	13	44	14	11	8	6	1	2	.	.	51	51	70	147	435
14	14	8	12	7	11	14	48	10	23	12	2	4	4	4	2	91	108	144	178	696
15	17	12	9	12	6	21	46	5	21	12	3	3	2	6	6	119	118	166	161	745
16	9	11	11	6	10	15	40	9	12	13	1	4	3	7	6	131	92	150	105	635
17	4	5	4	5	4	15	39	4	4	12	3	3	.	4	2	84	46	94	34	366
18	4	4	2	1	.	8	19	1	6	9	1	.	.	1	1	82	32	52	8	231
19	.	.	.	.	.	1	9	.	4	5	.	1	.	1	.	18	13	24	4	80
20	.	1	.	.	.	1	7	.	.	2	.	.	.	.	.	22	4	5	1	43
21	.	.	.	.	.	.	1	.	.	8	1	.	.	.	.	5	2	3	.	20
22	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	1	1	7	.	12
23	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	2	2	.	6
24	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
29	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
Total	61	43	50	45	46	119	335	67	103	88	21	16	16	23	20	688	543	846	921	4051
Average	14·6	15·5	14·6	14·4	14·1	14·3	14·4	13·2	14·6	16·2	14·2	15·5	13·4	15·8	14·9	15·4	14·9	14·9	13·3	14·6

APPENDIX 2

Hatching success of Perdix perdix *in England*

Size of clutch	No. of clutches in which all eggs hatched except														Total clutches	Total eggs	No. of eggs unhatched
	0	1	2	3	4	5	6	7	8	9	10	11	12	13			
4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	4	.
5	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	5	1
6	2	.	1	.	.	.	.	.	.	.	.	.	.	.	3	18	2
7	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	14	.
8	8	4	.	1	1	.	.	1	.	.	.	.	.	.	15	120	11
9	21	7	5	1	4	.	1	.	.	.	.	.	.	.	39	351	42
10	63	27	6	4	3	2	1	2	.	.	.	.	.	.	108	1,080	93
11	74	39	27	8	3	2	1	1	.	.	1	.	.	.	156	1,716	162
12	196	123	69	23	16	4	4	6	4	.	.	.	.	.	445	5,340	512
13	158	141	81	28	14	3	3	3	1	3	2	.	.	.	437	5,681	552
14	265	163	137	41	21	13	7	7	3	2	3	3	.	1	666	9,324	918
15	240	220	125	67	23	14	9	4	4	3	1	.	.	.	710	10,650	984
16	196	168	125	42	27	14	13	4	4	1	2	.	1	.	597	9,552	901
17	107	106	69	31	13	8	6	8	5	2	1	.	.	.	356	6,052	589
18	61	62	53	24	12	6	3	2	3	.	1	.	1	.	228	4,104	396
19	29	17	12	7	5	8	.	1	.	1	.	.	.	.	80	1,520	138
20	10	12	14	1	1	1	1	.	.	.	1	1	.	.	42	840	79
21	13	1	3	1	1	.	1	.	.	.	.	.	.	.	20	420	20
22	1	1	4	2	1	.	.	.	.	.	1	.	.	.	10	220	29
23	2	2	2	.	.	.	.	.	.	.	.	.	.	.	6	138	6
24	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	24	4
29	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	29	7
	1,449	1,094	733	281	146	75	50	40	24	12	13	4	2	1	3,924	57,202	5,446

APPENDIX 3

Differences in hatching success of Perdix perdix *in England*

Estate	Year	No. of eggs laid	% hatched
H5 Norfolk	1935	1,703	92·7
	1936	4,850	88·5
	1937	868	76·0
L8 Berks	1934	1,556	92·7
	1935	1,558	95·8
S1 Cambs	1931	10,382	89·3
	1933	8,049	87·6
	1934	12,515	91·3
	1935	11,456	92·5

REFERENCES

Baker, E. C. Stuart (1935). 'The nidification of birds of the Indian Empire', 4. London.

Bannerman, D. (MS.) 'A history of the birds of the Canary Islands.' (MS. in Brit. Mus. (Nat. Hist.).)

Collett, R. (1921). 'Norges fugle.' (Ved Orjan Olsen.) Oslo.

de Havre, G. C. M. (1928). 'Les oiseaux de la faune Belge', p. 426.

Errington, P. L. & Hamerstrom, F. N. (1937). 'The evaluation of nesting losses and juvenile mortality of the Ring-necked pheasant.' J. Wildlife Management, 1: 3–20.

Fatio, V. (1904). 'Faune des vertébrés de la Suisse', 2. (Histoire naturelle des oiseaux, II^me^ partie. Genève, etc.

Ford, E. B. (1940). 'Polymorphism and taxonomy.' In Huxley, J. S., 'The new systematics', 493–513. Oxford.

Hamerstrom, F. N. (1939). 'A study of the Wisconsin prairie chicken and sharp-tailed grouse.' Wilson Bull. 51: 105–20.

Jourdain, F. C. R. (1941). In Witherby, H. F. *et al.* 'The Handbook of British Birds', 5: 251. London.

Lack, D. (1947). 'The significance of clutch-size.' Ibis. (in the Press).

Leopold, A. (1933). 'Game management.' New York, etc.

McAtee, W. L. (1930). 'Propagation of upland game birds.' Fmrs' Bull. U.S. Dep. Agric. 1613: 1–60 (p. 57).

Merikallio, E. (1931). 'Kanalintujemme munamaarat.' Orn. Fenn. 8: 1–10.

Middleton, A. D. (1935). 'The population of partridges (*Perdix perdix*) in 1933 and 1934 in Great Britain.' J. Anim. Ecol. 4: 137–45.

Middleton, A. D. (1936*a*). 'Factors controlling the population of the partridge (*Perdix perdix*) in Great Britain.' Proc. Zool. Soc. Lond. 1935: 795–815.

Middleton, A. D. (1936*b*). 'The population of partridges (*Perdix perdix*) in Great Britain during 1935.' J. Anim. Ecol. 5: 252–61.

Moreau, R. E. (1944). 'Clutch-size: a comparative study, with special reference to African birds.' Ibis, 86: 286–347.

Moser, H. B. (1932). 'IV. The Hungarian partridge', pp. 29–33. In 'Partridge disease and its causes.' Ed. M. Portal and W. E. Collinge.

Prazak, J. P. (1898). 'Materialen zu einer Ornis Ost-Galiziens.' J. Orn., Lpz., 46: 197, 201.

Rey, E. (1912). 'Die Eier der Vögel Mitteleuropas.' 2nd ed. Gera-Untermhaus.

Yeatter, R. E. (1934). 'The Hungarian partridge in the Great Lakes region.' Bull. Mich. Sch. For. 5: 1–92 (p. 32).

Yocom, C. F. (1943). 'The Hungarian partridge *Perdix perdix* Linn. in the Palouse region, Washington.' Ecol. Monogr. 13: 169–201 (esp. p. 183).

AN ECOLOGICAL STUDY OF THE ENCHYTRAEID WORM POPULATION OF SEWAGE BACTERIA BEDS

FIELD INVESTIGATIONS

By T. B. REYNOLDSON, *Department of Zoology, University College of North Wales, Bangor*

(With Plate 1 and 5 Figures in the Text)

1. INTRODUCTION

The biology of the sewage bacteria bed has been extensively studied, but presentation of the results with emphasis on the applied aspect has partially obscured many features of ecological interest. Such a habitat possesses many advantages for ecological work which may be summarized as simplification of micro-habitats, relative stability of physical factors and restriction of the macro-fauna (Lloyd, 1935; Lloyd, Graham & Reynoldson, 1940); conditions which Elton (1927) has stressed as most suitable for the study of ecological principles. The bacteria bed has no close equivalent among natural habitats, but resembles the mud-flat and the high-water zone of decaying seaweed in many features. The presence of decaying organic matter is the ecological keynote of the bacteria bed. The present work originated as an applied problem and the conclusions reached on this aspect have already been published (Reynoldson, 1941, 1942). Here, it is proposed to describe results which have a more general biological interest.

The Enchytraeid worm *Lumbricillus* (= *Pachydrilus*; Černosvitov, 1937) *lineatus* Mull. is a very frequent inhabitant of bacteria beds and usually occurs in such vast numbers that it rivals the abundance of the so-called filter fly, *Psychoda alternata* Say (Reynoldson, 1939 *a*, *b*). In 1939 the author's attention was drawn to an unusual condition existing in the Huddersfield beds. Apparently, this worm was either very scarce or absent (Goldthorpe, 1939) and it was decided to investigate the problem of determining the actual size of the population and the causes of the depression. A similar paucity of insect species also occurs in these bacteria beds (Golightly, 1940). Preliminary observations seemed to confirm that the population of *Lumbricillus lineatus* in the Huddersfield beds was very small, but another species of Enchytraeid worm, *Enchytraeus albidus* Henle, a worm of wide geographical distribution, was found in some numbers. Thus the problem became more interesting since it involved a comparison of the ecology and physiology of two species of worms belonging to closely related genera (Stephenson, 1930, p. 772).

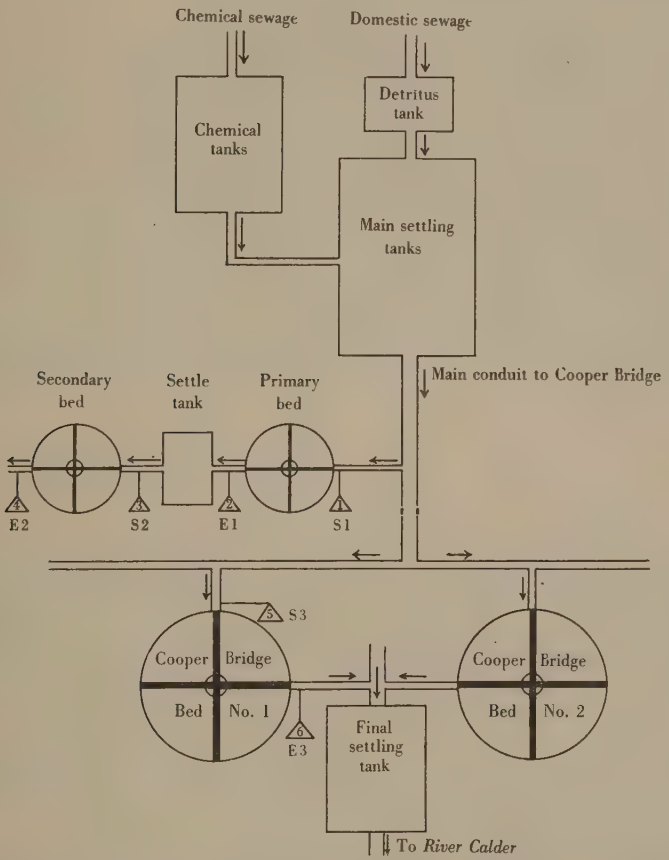
The present paper describes the field work and it will be shown that although *E. albidus* was the dominant Enchytraeid, its numbers were relatively small for such a habitat; the distribution within the beds was unusual and a marked seasonal cycle of abundance occurred. A second paper, mainly of applied interest, will give the results of laboratory experiments designed to provide information on certain factors which the field work had suggested to be affecting population size and distribution. With the object of explaining the unusual features noted above, a synthesis of field and laboratory data will be attempted in a third paper.

2. THE HUDDERSFIELD SEWAGE TREATMENT PLANT

A brief outline of the Huddersfield sewage treatment plant will clarify the presentation of the results (see Fig. 1). The bulk of the sewage is conveyed to the plant by a main sewer carrying domestic and textile wastes amounting to $8\frac{1}{2}$ million gallons per day. Two subsidiary sewers carry wastes amounting to $2\frac{1}{2}$ million gallons per day from large chemical works, thus giving a grand total of 11 million gallons per day. These rates apply specifically to the years 1939–40, conditions changing as the war progressed. It is the large proportion of chemical wastes which characterizes the Huddersfield sewage and renders it extremely difficult to treat satisfactorily. Before 1941, the chemical and domestic sewages were mixed at the entrance to the plant, but later they received separate preliminary settlement; Fig. 1 records the present day arrangement. After separate preliminary settlement the two sewages are combined and further settled in large tanks. From these tanks the sewage is directed in an open conduit to the bacteria beds situated some three miles down the valley. During working hours the sewage is 'limed' immediately after leaving the tanks to maintain the *p*H between values of 6·0 and 7·0. The large, circular, bacteria beds are raised above the ground; they measure 200 ft. in diameter and are 6–7 ft. deep. Each is built of pieces of clinker with a very irregular, pitted surface and measuring 3–6 in. in diameter. As will be shown in a later contribution, the nature of this clinker is important and it contrasts sharply with the smooth water-worn pebbles of which the Leeds beds

are constructed. The sewage is distributed over the bed surface by rotating machines (Pl. 1) and bacterial oxidation is active while it trickles downwards over the surface of the media as a thin film. Altogether, the Huddersfield bacteria beds provide 100,000 cu.yd. of filtering media. These main beds will be referred to

At the time of this investigation the Huddersfield Corporation authorities were engaged in research on what is termed the double filtration system. As the name implies, the sewage is treated first on one bed (Primary) at a higher rate than on routine beds and then on a second bed (Secondary) at a variable rate,



△ Sewage sampling points: S 1 Primary bed sewage; E 1 Primary bed effluent; S 2 Secondary bed sewage; E 2 Secondary bed effluent; S 3 Cooper Bridge sewage; E 3 Cooper Bridge effluent.

Fig. 1. A schematic plan of the Huddersfield Corporation sewage treatment plant (1942).

in the text as the Cooper Bridge beds after the locality in which they are situated. After passage through a bed a sewage is referred to as an effluent and accordingly that from the Cooper Bridge beds will be termed the Cooper Bridge effluent. Following a final detention in settling tanks, the effluent is passed to the River Calder.

with intermediate settling in a tank. Opportunity was taken to study the worm populations in these two model 20 ft. diameter beds, since conditions in them differed from those in the routine Cooper Bridge beds. It will avoid confusion if the terms to be applied to the sewage at the different treatment stages are stated now. The sewage treated in the Primary

bed (Pl. 1, photo. 1) is termed the Primary sewage and to all intents and purposes is the same as that applied to the Cooper Bridge beds; the latter is referred to as the Cooper Bridge sewage. The sewage leaving the Primary bed is termed the Primary effluent; that fed to the Secondary bed is termed the Secondary sewage and only differs from the Primary effluent in that it has had a detention period in a settling tank. The liquid flowing from the Secondary bed is referred to as the Secondary effluent. An outline plan of the system which also indicates sewage sampling points for laboratory experiments described in a further paper (in the Press), is given in Fig. 1. Pl. 1 shows the Primary and Secondary beds respectively and illustrates the method of sewage distribution by means of rotating machines. For a full account of the Huddersfield plant reference should be made to Goldthorpe & Nixon (1942) and Goldthorpe (1944).

3. FIELD METHODS

A bait consisting of 20 g. of scalded *Phormidium* (Cyanophyceae) contained in an open muslin bag was used to sample the worm populations. This method has been employed with satisfactory results in the Leeds beds (Reynoldson, 1939*a*) for estimating the relative abundance of *Lumbricillus lineatus*, a species of similar food habits to *Enchytraeus albidus* (Michaelson, 1927; Stirrup, 1913). The rapidity with which the worms were attracted into the food bags was noted during the Leeds work and it was found that stability was reached after 2 days. Although *Lumbricillus lineatus* is more active than *Enchytraeus albidus*, 14 days was ample time for stability to be reached between the number of the latter in the food bag and in the rest of the bed. A large proportion of the alga remained uneaten after 14 days and it seems unlikely that there was any general tendency for worms to leave the food bags within this period. This point was examined in the Leeds work and it was found that with a larger worm population and a greater proportion of alga consumed, there was still no tendency to leave the bags. The technique used to separate the worms from the alga in the laboratory was also similar, save that it was essential to sort and count as the copper sulphate forced them out, otherwise examination of the setae was necessary to distinguish *Lumbricillus lineatus* from *Enchytraeus albidus* (Ude, 1929). When alive, the two species can be separated by colour, *lineatus* being red-brown while *albidus* is white. Only worms about 6 mm. in length and over were counted, i.e. worms large enough to have reached maturity (Reynoldson, 1943). Identification of the two species was confirmed by the late Dr L. Černosvitov.

Populations were sampled in two of the Cooper Bridge beds to provide a measure of the reliability of the method. The food bags were set at three levels in each of the beds, 4–6, 12 and 36 in. beneath the surface. At the shallow zone the clinker was carefully removed to allow setting of the bag and then replaced. The spot was varied at each setting. Lidded pipes, 4 in. in diameter and sunk to the appropriate depth were used for the two lower levels (Fig. 2). The food bags rested on the clinker at the bottom of the pipe. In each bed, all three bags were changed fortnightly but at alternate weeks, so that, considering each bed separately, fortnightly estimates were available; considering the two beds as one unit, weekly estimates were achieved.

Similar methods were used in the Primary and Secondary beds except that the routine estimate at 36 in. was omitted; the latter zone in the Primary bed was sampled on seven occasions at approximately monthly intervals. In these two beds the routine bags were changed weekly.

In one of the Cooper Bridge beds sampling was commenced at the beginning of October 1939, but in the other not until the middle of November. It continued until the beginning of November 1940 in both. Sampling in the Primary and Secondary beds was started at the beginning of November 1939 and continued for 13 months. In March 1940 results from laboratory experiments suggested that the areas within the pipes, protected from a direct flow of sewage, might be unrepresentative of the rest of the bed. Accordingly, in April 1940 the sampling method in one of the Cooper Bridge beds, hereafter referred to as no. 1 bed, was modified. The lidded pipes were replaced by cylinders of strong perforated zinc, 4 in. in diameter and sunk into the bed; a second cylinder containing clinker was let down inside the outer sleeve. To set the food bag, the inner sleeve was raised, the bag let down on to the clinker by a piece of string and the inner sleeve replaced. Thus the conditions around the food bag simulated those for the rest of the bed except that the clinker in the cylinder was, perforce, of smaller diameter. A diagram of the two methods is shown in Fig. 2. A similar technique was used at the 12 in. level in the Primary and Secondary beds, but in the latter the lidded pipe was retained as a control. Thus independent comparisons of the two methods were available. In addition to this routine, sampling was also made during January and August 1940 in a small area of the Primary bed immediately surrounding the central column of the distributor. Food bags were set among the clinker of the top 6 in. in this part of the bed and removed after one week. The condition of the beds was noted each week and the air and bed temperatures recorded daily.

An estimate of the number of worms and cocoons washed out of the Secondary bed was made once weekly during the period March to April 1940 since laboratory experiment suggested that this factor was

Photo. 1. A view of the Primary bed showing the revolving machine distributing sewage; a pipe containing a thermometer is also shown towards the left, while at the extreme left there is a fly trap.

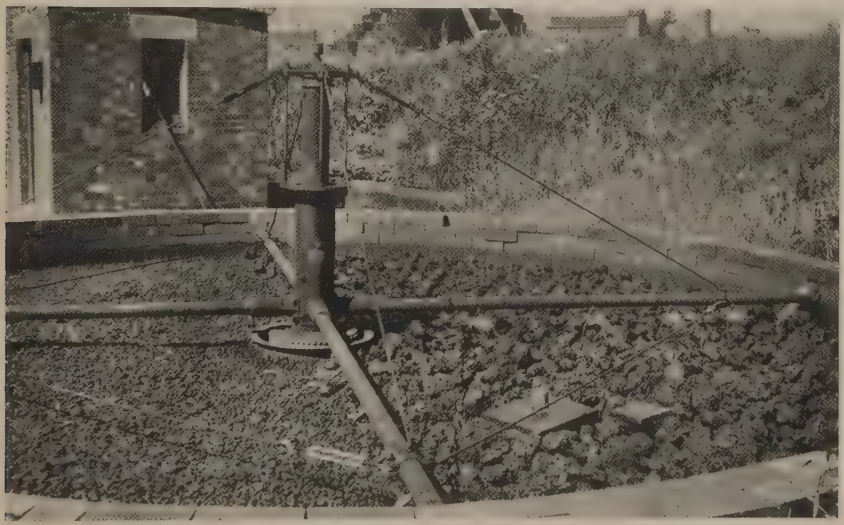


Photo. 2. A view of the Secondary bed again showing thermometer pipe and fly trap; the worm sampling was confined to the right half of the bed with the coarse surface media.

important. A net made with bolting silk sufficiently fine to retain the cocoons of *E. albidus* and carrying a jar, was used. This net was large enough to strain all the effluent leaving one-half of the Secondary bed. Each straining was made over a 5 min. period.

4. THE VALIDITY OF THE FIELD METHODS

The numbers of *Lumbricillus lineatus* collected in the Cooper Bridge beds were so small that they are ignored in the tests described here. In examining the validity of the results for *Enchytraeus albidus* it has been assumed that in broad terms each of the Cooper Bridge beds affords a similar environment for the worms and should therefore carry a similar population. The justification for the assumption is that both beds are structurally alike, treat the same sewage at approximately the same rate and are subject to the same weather variations. Moreover, the beds have been operating since 1910 and possible initial differences in the populations have had time in which to be smoothed out. On this reasoning, if the results obtained from each bed were representative then it should be possible to demonstrate first, that they were not drawn from numerically different populations, secondly, that they showed a general similarity in weekly variation. Unfortunately, the alternate sampling makes statistical comparison of the results for each bed difficult and it was necessary to set the weekly data from one bed backwards and forwards by one week to arrange the figures into pairs on a time scale. Thus, for example, in the case of the 12 in. level the number collected on 22 November (1190) was paired in one series with the number collected on the 15th (67) and in the second series with the number taken on the 29th (129). Similar manipulations were made in respect of the data for the 36 in. level, thus providing four series for testing. Students' t test (Fisher, 1942, para. 17) was applied to each series with the following results:

12 in. level (*a*) $n=21$, $t=1{\cdot}153$;
(*b*) $n=21$, $t=1{\cdot}27$.
36 in. level (*a*) $n=22$, $t=0{\cdot}919$;
(*b*) $n=22$, $t=0{\cdot}837$.

Although the values for t suggest a high degree of significance, they cannot be taken at face value because such manipulation of the data assumes that the worm population did not fluctuate markedly within the space of a week. On this point it has been calculated that only a small part of the variance was due to changes in one bed during a week, at most 0·3; this would not upset the significance obtained. The second difficulty arises because the standard deviation on which t is based is derived not only from random causes but also because the population in each bed did not keep exactly in step (Fig. 3). Therefore the results of the t test cannot be relied on too much. The similarity in the weekly fluctuations of worms in the two Cooper Bridge beds was also examined statistically by calculating the correlation coefficients. Adopting the same arrangement of figures as before, and therefore similar reservations, one set each for the 12 and 36 in. levels was used. In

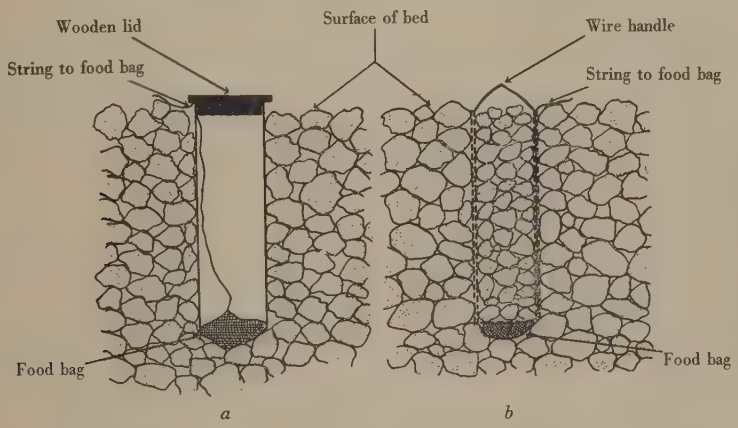


Fig. 2. The two methods of sampling the worm population. (*a*) First method—a hollow pipe with the food bag at the bottom. (*b*) Later method—two cylinders of perforated zinc, the inner of which contains clinker and can be lifted out by the wire handle.

the case of the former zone, the correlation coefficient had a value of $r = 0{\cdot}796$ ($n = 19$) which differs significantly from zero, i.e. a real degree of association between the number of worms taken in each bed seems likely. In the case of the 36 in. zone the correlation coefficient had a value of $r = 0{\cdot}404$ ($n = 19$) which just falls short of signifying a real association ($P = 0{\cdot}05$). The Appendix shows that the greatest divergence occurred in the early weeks of sampling and if the data for 29 November (956) and 6 December 1939 (48) are omitted, the correlation coefficient has a value of $r = 0{\cdot}513$ ($n = 18$) which suggests a real degree of association.

that the summer population of worms, as shown by the food bags, is more likely to be too large than too small and the reverse during the winter.

Before leaving this aspect of the work the effect of introducing a different sampling technique in Cooper Bridge no. 2 bed during April 1940 was tested by a statistical method similar to that used for comparing the results of sampling in the two beds. Using only data obtained after the introduction of the new method, comparison of the numbers collected in bed no. 1 and bed no. 2 yielded values of t equal to $0{\cdot}458$ ($n = 13$) for the 12 in. level and $0{\cdot}91$ ($n = 13$) for the 36 in. level. These results strongly suggest

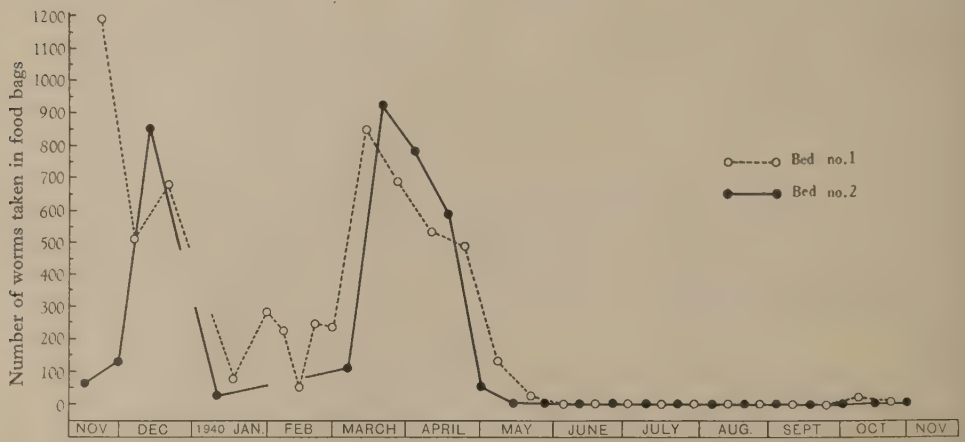


Fig. 3. Comparison of the number and fluctuations of *Enchytraeus albidus* in the Cooper Bridge beds nos. 1 and 2 at the 12 in. level.

Thus, although the statistical analyses cannot be fully satisfactory there seems no reason for doubting the validity of the sampling method. The agreement shown by the two beds is quite close, as Fig. 3 indicates—there was similar agreement at the 36 in. level. The significant correlation between fluctuations at the 12 and 36 in. level (§ 5 (*c*)), not subject to the above statistical limitations, also suggests the reliability of the method.

It is emphasized that this sampling method cannot be used to assess the absolute population of Enchytraeids but only to indicate the relative abundance. The criticism that such a method will tend to attract worms more powerfully during periods of food scarcity cannot be denied. However, in this particular case the worms showed a high winter population and a markedly lower summer population. Now it is well known that bacterial, fungal and algal growths which form the bulk of the worms' food are scarce during the summer owing to the activities of the insect larvae at this season. Therefore, it follows that the new technique made no significant difference to the number of worms collected. Comparison of the numbers taken in the Secondary bed by the two methods can be made from the Appendix. The fact that they are similar is apparent by inspection. The high proportion of noughts makes statistical analysis unprofitable.

5. THE FIELD DATA

(*a*) *The bacteria bed community*

The fauna of the Cooper Bridge beds and the seasonal changes in bed conditions have been described briefly by Golightly (1940). The macroscopic animals already known to breed in these beds are confined to the flies *Psychoda alternata* Say, *P. severini* Tonn., *P. cinerea* Banks and *Spaziphora* hydromyzina* Fall.; while the beetle *Cercyon ustulatus* (Preyssler) also finds the habitat suitable. Of these insects, only the

* [Often cited incorrectly as *Spathiphora* or *Spathiophora*.]

ordylurid *Spaziphora hydromyzina* is predaceous id it lives on the Psychodid flies; the remainder feed organic detritus and the growths of bacteria and ngi. In this community *Psychoda alternata* is arkedly dominant (Golightly, 1940). The macro-una of the Primary bed is restricted to this species hile that of the Secondary bed resembles the fauna the Cooper Bridge beds but has the following sects in addition: the flies, *Limosina* spp. (Bor-ridae), Staphylinid beetles and a beetle, *Helo-orus* sp. *Psychoda alternata* is again the dominant sect and outnumbers, by more than fifty times, the st of the insects put together. The conditions in e Primary and Secondary beds, including the terrelationship between the fauna and flora, have so been related in some detail (Reynoldson, 1941, 942). The main events are the building up of a eavy growth of the fungus *Oospora* during the winter onths and its rapid destruction by larvae of *Psychoda ternata* in the spring. These larvae continue to ntrol the volume of fungus during the warm months. omparison of the Huddersfield bacteria bed fauna ith those of other sewage works shows that it is uch restricted, particularly in the absence of hironomid species (Lloyd *et al.* 1940; Tomlinson, 945).

(*b*) *Total worm population*

The entire Enchytraeid population (including both ecies) of the Cooper Bridge beds was very much naller numerically than that found in bacteria beds other works, particularly those treating sewage latively free from strong trade wastes. The table low records figures of the average numbers of orms taken each week in the Knostrop beds (Leeds), e Oulton beds (near Leeds) and the Cooper Bridge ds (Huddersfield). In the case of the first and last these beds the results were averaged over a months' period, while the figures for Oulton were ken from one collection in the case of the 6 and in. levels, but were based on the average of six llections at the 12 in. level made during June and ly 1940. The Knostrop figures which refer to orms in the surface growth of alga are not strictly mparable to those at the 6 in. level for Cooper idge and Oulton, but they serve to show the con-ast with Cooper Bridge. Actually, the worms at the in. level at Knostrop were more abundant than in e surface growth (Reynoldson, 1939*a*) and if the rmer data were available they would only indicate e difference more sharply.

Observations made at the Temple Newsham and the Rodley beds (near Leeds) showed a similar Enchytraeid fauna to that of Knostrop. These data make it abundantly clear that not only are the Cooper Bridge beds unsuitable for *Lumbricillus lineatus* but even *Enchytraeus albidus* is able to exist there in relatively small numbers compared with Enchytraeids in other beds. In a further paper presenting the laboratory evidence it will be shown that the scarcity of *Lumbricillus lineatus* results from the high proportion of trade wastes in the Huddersfield sewage; *Enchytraeus albidus* is much more resistant.

The second difference brought out by these figures concerns the vertical distribution of the worms. Taken over a lengthy period, the maximum concentration occurred in the surface layers of media at Knostrop and also probably at Oulton, whereas at Cooper Bridge the worms were fewest at the surface. It should be noted that this avoidance of the upper zone also occurred in the Secondary bed at Huddersfield. The Knostrop and Cooper Bridge populations agreed in showing an approximately equal concentration at their respective 12 and 36 in. levels. The high number at the 36 in. level in the Oulton beds was probably an anomaly produced by one sample.

(*c*) *The seasonal variation*

The weekly figures afforded by the sampling are recorded in the Appendix for all beds except the Primary, where worms were virtually absent; Fig. 4 records the same figures graphically. (Data for *Lumbricillus lineatus* are omitted from the graphs of the Cooper Bridge beds since the numbers were small and the incidence low.) It clearly shows that in all beds and for both species of worm there was a relatively high winter population, concentrated at or below the 12 in. level. This population was reduced rapidly during April and May 1940 and remained at a low level during the summer. In the case of *Enchytraeus albidus* recovery in all beds began during September and October 1940 and although actual figures are not available, observation showed that this increase proceeded until the approximate winter population of the previous year had been attained. Such a fluctuation was also observed in 1941 and 1942 and is one of the most interesting results of this investigation. A similar recovery was not detected in the case of *Lumbricillus lineatus*.

Considering for the moment only the Cooper Bridge beds, the data obtained during October and November 1939 suggest a building up of the winter

Sewage plant	6 in. level	12 in. level	36 in. level	Species
Knostrop	2040*	1025	1065	All *Lumbricillus lineatus*
Oulton	7500	1182	7000	Majority (> 99 %) *L. lineatus*
Cooper Bridge	4	200	168	Majority *Enchytraeus albidus*

* Worms in 1 sq.ft. of alga.

population from an initial low summer population. The rate of increase can be rapid, since at 10° C. the worm develops from the egg to a mature adult in 68 days, at 15° C. in 40 days. At these respective temperatures one worm can produce three and five fertile eggs in the space of 5 days (Reynoldson, 1943). The irregularity of the figures for worms collected during December 1939 and January 1940 is difficult to explain. During February there was a marked decline at all levels which seemed therefore to reflect some general change. In fact, at this time sampling had to be suspended in no. 2 bed owing to ponding, i.e. blockage of the bed with the formation of surface pools. It may be that bed conditions became generally unfavourable at this time with a consequent absolute reduction in numbers or a migration to lower levels. It was not a phenomenon common to all the beds at Huddersfield because there was no February reduction in the Secondary bed. If in fact the decline was due to ponding, this contrast might be expected, since the Secondary bed never ponded during the 12 months it was under observation.

The population was relatively steady during March and most of April and the number of worms in the shallow zone showed a maximum during this period. The sharp decline began in the last week of April and by the end of May there were relatively few worms in the beds. This decline was coincident with the introduction of the new sampling technique in no. 1 bed, but the fact that it also occurred in no. 2 bed nullifies any suggestion that there was a connexion, a conclusion supported by statistical analysis (§ 4). It should be noted that this decline had already set in before the period of creosote treatment (see Fig. 4). Recovery in September seemed to start from the 36 in. level and this may be a constant feature of the seasonal change. The presence of worms, though in reduced numbers, at the 36 in. level throughout the summer seemed to be a real difference from conditions at the 12 in. level. They probably represented the 'nucleus' from which the winter population was built up. The curves (Fig. 4) representing the number of worms living at the 12 and 36 in. zones in the Cooper Bridge beds are strikingly similar and give a correlation coefficient of $r=0{\cdot}713$ ($n=46$) which has a high degree of significance. This suggests that variations in abundance represented real pulsations in the population rather than local migration, at least in the upper 36 in. of clinker. Such changes were also reflected at the bed surface.

The data for the Secondary bed showed, in broad terms, a similar story although the winter recovery was delayed. The trend was more irregular and this may result from the much smaller absolute size of the Secondary bed population. This irregularity and smaller population associated with the Secondary bed will be examined critically in another paper. Again, it was noticed that the curves for the worms collected from the 6 and 12 in. levels were similar in shape. Statistical examination of the data over the four months February to May 1940 gave a correlation coefficient of $r=0{\cdot}393$ ($n=16$) which failed to give significance to the relationship. Therefore, we are not justified in concluding that the fluctuations in numbers represented pulsations of the population as a unit in this bed. The population of *L. lineatus* in the Secondary bed was of a similar size to that of *Enchytraeus albidus*, a condition quite different from that found in the Cooper Bridge beds. It is perhaps noteworthy however that *Lumbricillus lineatus* showed no winter recovery and moreover the decline in spring was more catastrophic, coinciding with the introduction of the new trapping method. There is one interesting feature concerning the appearance of *L. lineatus* in the Huddersfield beds which may easily escape notice. Namely, this species was recorded on 15 separate occasions in the Cooper Bridge beds and nine of these were during April and March 1940. Reference to the Secondary bed shows that it was precisely at this time that *L. lineatus* reached its maximum density there. It seemed as though a condition common to all the Huddersfield beds had arisen to produce this result.

(*d*) *The worm population of the bed centre*

The results of sampling in the small part of the Primary bed surrounding the central column are interesting. This area, approximately 12 in. in diameter, lay outside the direct range of the innermost jet of sewage (Pl. 1 *a*), but the clinker always remained damp, partly from condensation of water vapour, rain and occasional splashes of sewage. Consequently, conditions differed from those of the rest of the bed with only slight bacterial and fungal growths and little organic debris. The following number of worms were taken from the food bags:

Date 1940	No. of *Enchytraeus albidus*	No. of *Lumbricillus lineatus*
3 January	8	1
3 January	27	4
3 January	6	0
14 August	4	1
21 August	3	0

Clearly, a small population of both species was existing in this 'micro-habitat'. It should be noted that both species were unable to occupy the remainder of this bed and also that *Enchytraeus albidus* was found here among the topmost clinker during August, a period when they could not be found in the corresponding zone of any of the other beds treating sewage.

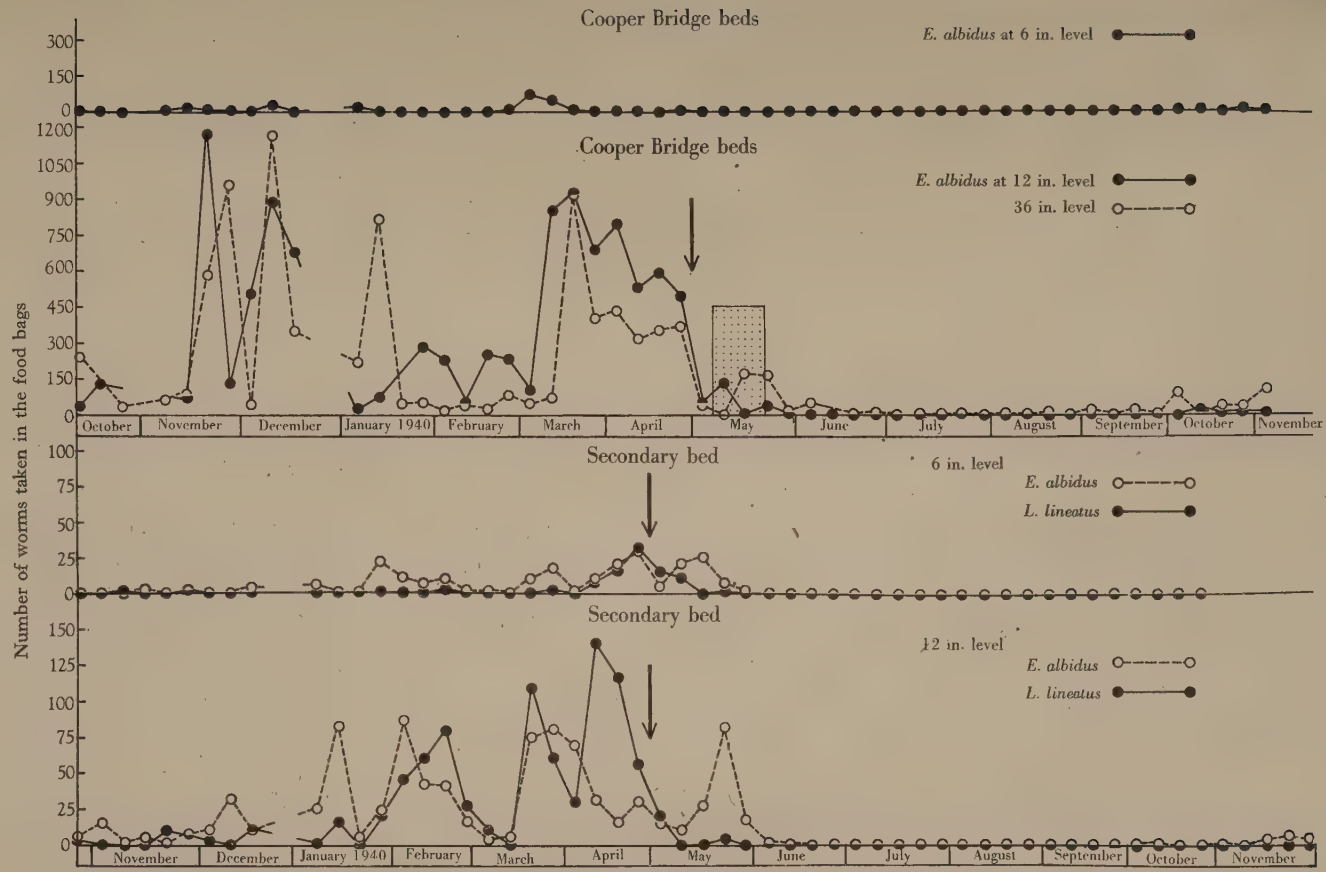


Fig. 4. A graphical record of the worms collected from the food bags at the 6, 12 and 36 in. levels in the Cooper Bridge and Secondary beds. The arrows indicate the time at which the sampling technique was modified; the stippled area represents the period of creosote treatment of the Cooper Bridge beds.

(*e*) *The breeding season*

Observations on Enchytraeid worms in general suggest that winter is the breeding season in so far as a period can be delimited (Stephenson, 1930, p. 435), but the problem has not been systematically studied. Observation of *Lumbricillus lineatus* inhabiting the Knostrop beds supported the suggestion (Reynoldson, 1939*b*), but in view of the definite seasonal occurrence of *Enchytraeus albidus* at Huddersfield more precise information was required on this point. Therefore, in addition to counting the worms entering the Cooper Bridge food bags, the number of cocoons which had been deposited therein was also recorded from January 1940 onwards. The bag with the greatest number of worms was always chosen for the cocoon count so that the population sample was as large as possible. It seemed most reasonable to relate the number of cocoons thus obtained to the number of worms taken in the bag, since *E. albidus* is a rather sluggish animal and once it had entered the food bag it would not tend to leave it. Thus, the proportion of cocoons to worms would indicate approximately the relative breeding activity of the population at the time. The larger the sample of worms, the more representative the result might be expected to be and all data for less than twenty worms have been discarded as insufficiently reliable. The results are recorded in Table 1 and Fig. 5. They indicate that breeding activity was at a peak during the winter and the early spring. A rapid decline occurred in May and June and it seemed reasonable to infer from the scarcity of worms that the summer was a quiescent period. The recovery of the bed population in October is therefore seen to be coincident with an increase in breeding activity. These quantitative data bear out the observation that breeding is more active during the colder months. Winter breeding is sufficiently infrequent to merit comment. It has been recorded for the group of animals which inhabit the shallow, stagnant water of harbours and in this case Lo Bianco (Flattely & Walton, 1922, p. 248) suggested that it might be an adjustment to avoid the peak period of putrefaction. The habitats of Enchytraeid worms are also subject to periods of putrefaction, but the danger of desiccation during the summer in areas bordering streams, ponds, lakes and on the seashore may be a more important factor promoting a winter breeding season; the thin, permeable, wall of the cocoons exposes the eggs to the danger of drying up.

Table 1. *The record of the cocoons and worms* (Enchytraeus albidus) *obtained from the food bags, on which breeding activity is based. The data recorded refer only to food bags which contained more than twenty worms*

Date 1940	Bed no.	Depth (in.)	No. of cocoons	No. of worms	Cocoons/worms (%)
31 January	1	12	43	286	15
7 February	1	12	53	233	23
14 ,,	1	12	4	52	8
21 ,,	1	12	23	248	9
28 ,,	1	12	76	237	32
6 March	2	12	34	107	32
13 ,,	1	12	188	850	22
28 ,,	1	36	239	404	59
3 April	2	36	320	433	74
10 ,,	1	36	157	316	50
17 ,,	2	12	64	590	11
24 ,,	1	12	196	490	40
1 May	2	12	0	51	0
1 ,,	2	36	0	41	0
8 ,,	1	12	18	128	14
15 ,,	2	36	8	172	5
22 ,,	1	36	24	162	15
5 June	1	36	3	49	6
4 September	2	36	13	21	62
18 ,,	2	36	1	26	4
2 October	2	36	25	94	27
16 ,,	2	36	17	41	41
23 ,,	1	36	23	42	55
1 November	2	36	42	104	40

(f) Results from straining the Secondary effluent

The number of worms and cocoons strained from the Secondary effluent by the net are recorded in Table 2. These figures represent losses during a period of 5 min. and it does not tax the imagination severely to appreciate the daily loss to a population as small as that of *E. albidus* in this bed. The full significance of this drain in relation to population size and the seasonal cycle will be discussed in a later paper.

Table 2. *A record of the number of worms and cocoons* (Enchytraeus albidus *and* Lumbricillus lineatus) *strained from the Secondary effluent during a 5 min. period*

Date 1940	Adult worms		Immature worms		Cocoons	
	E. albidus	*L. lineatus*	*E. albidus*	*L. lineatus*	*E. albidus*	*L. lineatus*
6 March	12	0	0	0	61	0
13 ,,	16	0	0	0	145	0
28 ,,	2	0	101	2	181	2
10 April	6	0	127	0	89	3
24 ,,	6	0	54	0	15	0
Totals	42	0	282	2	491	5

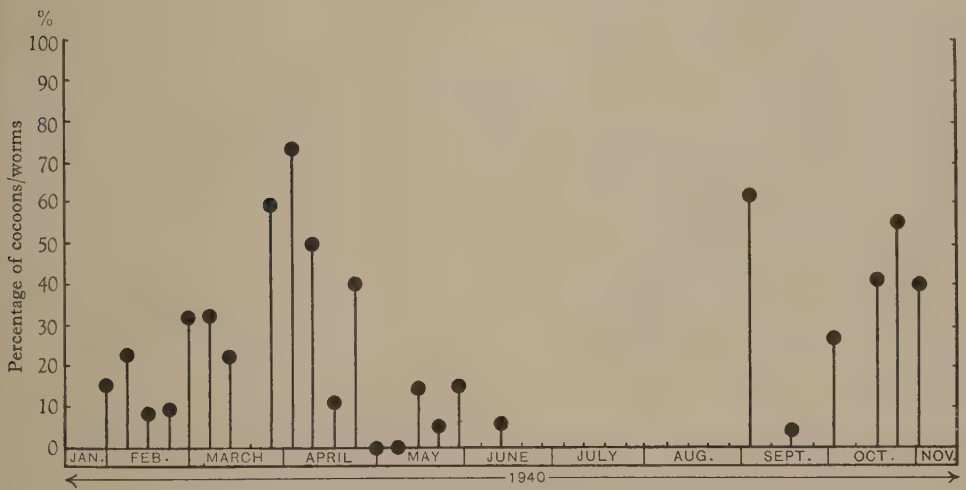


Fig. 5. The seasonal variation in reproductive activity of *Enchytraeus albidus* based on the ratio of cocoons to worms collected from the food bags.

6. SUMMARY

1. The relative size, distribution and seasonal incidence of the Enchytraeid worm population of the Huddersfield Corporation sewage bacteria beds have been determined by a weekly sampling technique. Three beds, each representing a different phase in the treatment of sewage, were studied. They showed numerically different populations, but the general features were in agreement.

2. An outline description of the Huddersfield sewage plant is given. The sewage of this drainage area is characterized by a high proportion of chemical trade wastes and differs markedly from the more usual domestic sewages.

3. The method of sampling the worm population is described and statistical analysis of the results indicates that the technique provided a reliable measure of the population.

4. The common bacteria bed Enchytraeid worm, *Lumbricillus lineatus* Mull. was scarce in these beds; another species, *Enchytraeus albidus* Henle, not previously recorded from this habitat, was more abundant.

5. The total Enchytraeid worm population was much smaller than is usual for bacteria beds; the

vertical distribution of the worms also differed in that the population was concentrated below the top 12 in. of clinker.

6. A marked seasonal variation in population size was observed, with a maximum during the winter and a minimum during the summer. Sampling in a small area of one of the beds immediately surrounding the central distributor revealed important differences in the population compared with that of the rest of the bed.

7. Observations on the reproductive activity of *E. albidus* showed that the main breeding season occurred during October to April inclusive.

8. Straining the sewage immediately after passage through the bed demonstrated a considerable loss to the population of *E. albidus* by the washing out of worms and cocoons.

7. ACKNOWLEDGEMENTS

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REFERENCES

Černosvitov, L. (1937). 'System der Enchytraeiden.' Bull. Ass. Russe Rech. Sci. à Prague, Vol. 5 (10), Sect. Sci. Nat. et Mat. No. 34: 263–95.

Elton, C. (1927). 'Animal ecology.' London.

Fisher, R. A. (1942). 'The design of experiments.' 3rd ed. London.

Flattely, F. W. & Walton, C. L. (1922). 'The biology of the sea-shore.' London.

Goldthorpe, H. H. (1939). Discussion on paper entitled 'The role of macro-organisms in bacteria beds.' J. Proc. Inst. Sewage Purif.: 169–72.

Goldthorpe, H. H. (1944). 'Descriptive notes—county borough of Huddersfield Sewage Works Dept.' J. Proc. Inst. Sewage Purif.: 94–101.

Goldthorpe, H. H. & Nixon, J. (1942). 'A report upon the treatment of sewage on percolating filters at Huddersfield.' J. Proc. Inst. Sewage Purif.: 101–15.

Golightly, W. H. (1940). 'Factors influencing the abundance and size of *Psychoda* species in sewage bacteria beds.' Ann. Appl. Biol. 27: 406–21.

Lloyd, Ll. (1935). 'The bacteria beds of sewage works as an environment for insects.' Proc. R. Ent. Soc. Lond. 10: 34–9.

Lloyd, Ll., Graham, J. F. & Reynoldson, T. B. (1940). 'Materials for a study in animal competition. The fauna of the sewage bacteria beds.' Ann. Appl. Biol. 27: 122-50.

Michaelson, W. (1927). 'Die Tierwelt der Nord- und Ostsee.' Teil 6c, Leipzig.

Reynoldson, T. B. (1939*a*). 'Enchytraeid worms and the bacteria bed method of sewage treatment.' Ann. Appl. Biol. 26: 138–64.

Reynoldson, T. B. (1939*b*). 'On the life-history and ecology of *Lumbricillus lineatus* Mull. (Oligochaeta).' Ann. Appl. Biol. 26: 782–99.

Reynoldson, T. B. (1941). 'The biology of the macrofauna of a high-rate double filtration plant at Huddersfield.' J. Proc. Inst. Sewage Purif.: 109–24.

Reynoldson, T. B. (1942). 'Further studies on the biology of a double filtration plant at Huddersfield.' J. Proc. Inst. Sewage Purif.: 116–39.

Reynoldson, T. B. (1943). 'A comparative account of the life cycles of *Lumbricillus lineatus* Mull. and *Enchytraeus albidus* Henle in relation to temperature.' Ann. Appl. Biol. 30: 66–6.

Stephenson, J. (1930). 'The Oligochaeta.' Oxford.

Stirrup, H. H. (1913). 'A descriptive study of an Oligochaete worm of the family Enchytraeidae; with an appendix on certain commensal Protozoa.' Proc. Zool. Soc. Lond. 300–21.

Tomlinson, T. G. (1945). 'Investigations into fly populations of percolating filters.' J. Proc. Inst. Sewage Purif. (in the Press).

Ude, H. (1929). 'Oligochaeta.' Tierwelt Deutschlands, Teil 15.

APPENDIX

The weekly record of the numbers of *Enchytraeus albidus* and *Lumbricillus lineatus* taken in the food bags.* Figures for *L. lineatus* in the Cooper Bridge beds in parentheses; figures from control sampling in the Secondary bed in italics.

Date 1939	Cooper Bridge beds				Secondary beds			
					6 in. level		12 in. level	
	Bed no.	6 in. level	12 in. level	36 in. level	*E. albidus*	*L. lineatus*	*E. albidus*	*L. lineatus*
11 Oct.	1	2	33	240	—	—	—	—
19 ,,	1	1	124	—	—	—	—	—
26 ,,	1	0	—	34	0	0	6	3
2 Nov.	—	—	—	—	0	0	15	0
8 ,,	1	5 (1)	—	60	0	1	2	0
15 ,,	2	25	67 (6)	88 (5)	2	0	4	0
22 ,,	1	12	1190	582	0	0	2	8
29 ,,	2	5	129	956 (13)	1	1	7	7
6 Dec.	1	1	509	48	0	0	10	3
13 ,,	2	29	850	1182 (3)	0	0	32	0
20 ,,	1	0	676	350	3	0	8	9
1940								
10 Jan.	2	14	22	216	4	0	25	1
17 ,,	1	0	82	809	0	0	82	16
24 ,,	2	0	—	39	0	0	5	0
31 ,,	1	0	286	49	21	0	24	21
7 Feb.	1	0	233	14	9	0	87	45
14 ,,	1	0	52	38	6	0	42	60
21 ,,	1	0	248	25	8	1	42	78
28 ,,	1	7	237	83	1	0	17	27
6 Mar.	2	68	107	42	1	0	3	10
13 ,,	1	42	850	67	0	0	5	0
20 ,,	2	5 (1)	923 (32)	937 (8)	9	0	75	109
28 ,,	1	0	688 (4)	404	17	2	80	60
3 Apr.	2	1	788 (10)	433 (11)	1	0	69	29
10 ,,	1	1	530	316 (3)	10	7	31	140
17 ,,	2	0	590	357	20	16	16	117
24 ,,	1	2	490	365 (2)	28	32	30	56
1 May	2	0	51 (1)	41	New sampling technique introduced 24 April			
1 ,,	New sampling technique introduced into bed no. 1 on 1 May				4	15	14	20
8 ,,	1	0	128	0	20	10	10	0
15 ,,	2	0	3	172	25	0	27	0
22 ,,	1	0	33	162	7	1	82	3
29 ,,	2	0	2	16	2	0	17	0
5 June	1	0	0	49	0	0	1	1
12 ,,	2	0	0	—	0	0	0 *0*	0 *2*
19 ,,	1	0	0	1	0	0	0 *0*	0 *0*
26 ,,	2	0	0	12	0	0	0 *0*	0 *0*
3 July	1	0	0	0	0	0	0 *0*	0 *0*
10 ,,	2	0	0	2	0	0	0 *0*	0 *0*
17 ,,	1	0	0	1	0	0	0 *0*	0 *0*
24 ,,	2	0	0	1	0	0	0 *0*	0 *0*
31 ,,	1	0	0	0	0	0	0 *0*	0 *0*
7 Aug.	2	0	0	1	0	0	0 *0*	0 *0*
14 ,,	1	0	0	1	0	0	0 —	0 —
21 ,,	2	0	0	7	0	0	0 —	0 —
28 ,,	1	0	0	0	0	0	0 —	0 —
4 Sept.	2	0	0	21	0	0	0 —	0 —
11 ,,	1	0	0	0	0	0	0 *0*	0 *0*
18 ,,	2	0	0	26	0	0	0 *0*	0 *0*
25 ,,	1	0	0	1	0	0	0 *0*	0 *0*
2 Oct.	2	2	0	94 (8)	0	0	0 *0*	0 *0*
9 ,,	1	1	22	0	0	0	1 *0*	0 *0*
16 ,,	2	0	1	41	0	0	0 *0*	0 *0*
23 ,,	1	6	6	42	0	0	0 *1*	0 *0*
1 Nov.	2	1	2	104	—	—	1 *0*	0 *0*
7 ,,	—	—	—	—	—	—	0 *2*	0 *0*
13 ,,	—	—	—	—	—	—	3 *2*	0 *0*
20 ,,	—	—	—	—	—	—	6 *1*	0 *0*
27 ,,	—	—	—	—	—	—	3 *7*	0 *0*

* Primary bed data omitted—1 *E. albidus*, 0 *L. lineatus* taken in 13 mth. sampling.

THE DURATION OF THE EGG STAGE IN THE RACES OF *ANOPHELES MACULIPENNIS* MEIGEN (DIPTERA, CULICIDAE)

By D. S. KETTLE and G. SELLICK, *Royal Army Medical Corps*

(With 2 Figures in the Text)

1. INTRODUCTION

The data, presented in this paper, were collected in Italy in the spring of 1945 during an investigation (to be published later) into the cessation of hibernation and the commencement of full reproductive activity in the races* of *Anopheles maculipennis*. In the course of this work an estimate was required of the duration of the aquatic stages—egg, larva, pupa—at the low prevailing spring temperatures, in order to forecast the probable date when newly emerged adults would begin to appear. Since eggs were readily obtainable and their development was independent of an adequate food supply in the external medium, their duration formed the simplest basis for this estimate, assuming that the egg stage is proportional to the total duration of the aquatic stages.

At the commencement of the work it was not suspected that at a given temperature there would be any difference in the duration of the egg stage in the various races of *A. maculipennis*, but in the course of the experiments it was noticed that eggs of *A. m. maculipennis* (= *typicus*) often hatched sooner than eggs of *A. m. labranchiae* laid at the same time. This was more marked at low temperatures when the eggs of *A. m. labranchiae* hatched in about 13 days, whilst those of *A. m. maculipennis* were taking about 10 days. Also, in bowls containing eggs of *A. m. maculipennis* and those of other races, there were often two distinct periods of hatching. Unfortunately, this was never investigated to see if it were due to one race hatching before the other, as the work was brought to an abrupt end by the return of one of the authors to the United Kingdom. When the results were analysed, a statistically significant difference was revealed between the rate of egg development in *A. m. maculipennis* and *A. m. labranchiae*. This vitiated numerous observations on mixed egg batches.

The races of *A. maculipennis* are remarkably similar in their morphology, but show considerable differences in their physiology, of which the most important from the malariologist's point of view is that some races such as *A. m. labranchiae* are androphilic, whilst others such as *A. m. maculipennis* are zoophilic (Missiroli, Hackett & Martini, 1933). Also, at the onset of winter some hibernate whilst others manifest the phenomenon of 'gonotrophic dissociation', i.e. the continuance of normal feeding without the usual resultant maturation of the ovaries. For example, in Holland, *A. m. messeae* accumulates a large amount of fat in the adipose tissue and seeks a cold dark shelter where it remains quiescent until the spring, whilst *A. m. atroparvus* enters warm houses and feeds repeatedly throughout the winter, but its ovaries do not mature (Swellengrebel, 1929). The larvae of the various races differ in their ability to withstand high concentrations of sea water. Thus, Bates (1939) found that *A. m. atroparvus* could successfully develop in 30% sea water, whilst *A. m. maculipennis* and *A. m. messeae* could withstand little more than 20%. The experiments recorded in this paper point to yet another physiological difference between the races of *A. maculipennis*, and since there is little likelihood of our repeating them in greater detail the results are given here in full in the hope that they may form the starting-point for a more adequate investigation.

Routine Service duties in the Army unit to which the authors were attached prevented continuous observations and conditioned the nature of the experiments.

2. TECHNIQUE

Wild caught female *Anopheles maculipennis* were placed in mosquito cages (6 × 6 × 6 in.) containing small glass dishes of water, on which they readily oviposited. This method of obtaining eggs was very simple and satisfactory except that when the collection had been made in a locality where the *A. maculipennis* population belonged to more than one race, the eggs of the different races were often inextricably mixed.

Oviposition took place in an incubator, at 25° C. during February and March, and at room temperature from April to June, but no correction similar to that used by Powsner (1935) has been made for the development of the eggs in the incubator, since the duration of the egg stage was only calculated to the nearest whole day.

The glass dishes were removed each morning at 09.00 hr. and the number of egg batches of each variety estimated separately by each author; at first another examination was made at 17.30 hr. but as

* For a discussion of the systematic position of these races of *Anopheles maculipennis*, see Bates (1940) and Mayr (1942, pp. 205–6).

very few eggs were laid in the day time this was discontinued. There was close agreement between each person's estimates, and on three occasions, as an additional check, a number of females were placed in a mosquito cage and allowed to oviposit on water in glass dishes, whilst an equal number of females in the same stage of ovarial development, as can be judged from the external appearance, were isolated in test-tubes lined with damp filter paper for oviposition. The percentage of females which laid eggs in test-tubes was of the same order as that estimated to have laid in the glass dishes, i.e. 40–45 %.

Table 1. *Incubation periods of eggs of* A. m. labranchiae *at different temperatures*

Date	Mean daily temperature ° C. Maximum	Minimum	Mean	Incubation period in days
26 February	10·7	10·3	10·5	11
26 ,,	10·8	10·0	10·4	13
26 ,,	10·8	10·0	10·4	13
26 ,,	10·8	10·0	10·4	14
28 ,,	11·2	10·0	10·6	14
1 March	11·2	10·0	10·6	13
2 ,,	11·1	10·1	10·6	10
3 ,,	11·6	10·0	10·8	13
4 ,,	11·5	9·9	10·7	11
4 ,,	11·9	9·9	10·9	14
15 ,,	13·3	10·5	11·9	9
17 ,,	13·8	11·0	12·4	11
26 ,,	14·8	12·8	13·8	7
7 April	15·0	13·6	14·3	5
7 ,,	15·0	13·6	14·3	5
9 ,,	15·2	13·2	14·2	6
10 ,,	15·8	13·4	14·6	6
12 ,,	16·7	14·3	15·5	6
14 ,,	17·0	14·4	15·7	3
14 ,,	17·4	14·8	16·1	5
17 ,,	18·1	16·1	17·1	5
18 ,,	17·9	16·3	17·1	4
19 ,,	17·9	16·5	17·2	5
4 May	17·1	14·1	15·6	4
4 ,,	18·1	15·1	16·6	6
6 ,,	19·4	15·4	17·4	4
7 ,,	19·9	15·9	17·9	3
15 ,,	25·4	22·8	24·1	2
15 ,,	25·4	22·8	24·1	2
16 ,,	25·6	23·2	24·4	2
16 ,,	25·6	23·2	24·4	2
17 ,,	25·3	23·3	24·3	2
17 ,,	25·3	23·3	24·3	2
17 ,,	25·3	23·3	24·3	2

The egg batches, varying in number from one to six, were transferred to enamel bowls and kept in the laboratory in the shade, where they were inspected during the day from 09.00 to 17.30 hr. as frequently as other work permitted, and a note made of the day on which the eggs hatched. For practical purposes the demarcation between successive days was not midnight but the time the laboratory closed, i.e. 17.30 hr. For example, eggs laid during the night 7–8 April were removed from the cage on the morning of the 8th, and hatched some time between 17.30 hr. 13th and 17.30 hr. 14th; therefore, the duration of the egg stage was 6 days. In practice it was observed that very few eggs hatched during the night. When a large number of egg batches of one variety were obtained, more than one experiment was set up, and hence the multiplicity of results in Tables 1–3.

Table 2. *Incubation periods of eggs of* A. m. maculipennis *at different temperatures*

Date	Mean daily temperature ° C. Maximum	Minimum	Mean	Incubation period in days
25 February	10·6	10·2	10·4	12
7 March	11·7	9·7	10·7	8
15 ,,	13·2	10·4	11·8	8
15 ,,	13·2	10·4	11·8	8
27 ,,	15·1	13·1	14·1	7
1 April	16·1	14·1	15·1	6
2 ,,	16·3	14·1	15·2	5
3 ,,	16·3	14·1	15·2	5
4 ,,	16·2	14·2	15·2	5
4 ,,	16·2	14·2	15·2	5
5 ,,	16·3	14·3	15·3	4
7 ,,	15·2	13·4	14·3	6
7 ,,	15·4	14·0	14·7	3
9 ,,	15·1	13·1	14·1	5
14 ,,	17·5	14·7	16·1	4
28 ,,	17·4	16·0	16·7	4
29 ,,	17·3	15·9	16·6	4
16 May	25·5	23·3	24·4	2
30 ,,	21·6	20·6	21·1	3
31 ,,	21·8	20·4	21·1	3
1 June	21·6	20·2	20·9	3
2 ,,	22·3	20·7	21·5	3

A maximum and minimum thermometer was placed beside the bowls containing the eggs and read every morning at 09.00 hr. The daily range of temperature in ° C. was small, and averaged 2·2° for all the months, with a minimum of 0·6° and a maximum range of 5·0°. During the months of April, May, June and July there was very little difference between the mean daily temperature ranges, which were 2·5°, 1·9°, 2·3°, and 2·1° respectively. The average of the maximum and minimum temperatures for each day was taken as the mean daily temperature.

The *A. maculipennis*, from which eggs were obtained for these experiments, were mainly collected within 30 miles of Rome, except that all the *A. m. melanoon* and approximately one-third of the *A. m. labranchiae* were captured near Monte San Biago railway station, which is situated at the southern end of the Pontine marshes, 70 miles south of Rome.

3. RATE OF DEVELOPMENT OF EGGS OF *A. MACULIPENNIS* RACES

A number of theoretical formulae have been proposed to express the relationship between the time taken to complete a biological reaction and the temperature at which it takes place. Thus, Bělehrádek (1926) proposed the general formula

$$\log y = \log a - b \log x, \qquad (1)$$

where y represents the time taken for a biological reaction to be completed at $x°$ C., and a and b are constants. This formula assumes that as the temperature is increased in geometrical proportion by a certain factor, so the time taken will steadily decrease in like proportion by another factor, and the ratio between the factors will be the constant b. This assumption is true for the greater part of the temperature range over which biological reactions proceed, but at the extremes of high and low temperatures this simple relationship between temperature and time no longer applies. To overcome this divergence, at the biological extremes of temperature, between experimental results and derived formulae Davidson (1944) proposed a formula of the general type

$$y = \frac{1 + e^{a-bx}}{K}, \qquad (2)$$

where y represents the time required for development to be completed at a given temperature x; K, a and b are constants, and e is the base of the natural logarithms. The constant K is calculated from the expression

$$K = \frac{2P_1P_2P_3 - P_2^2(P_1 - P_3)}{P_1P_3 - P_2^2},$$

where P_1, P_2 and P_3 are values for $100/y$, i.e. the average percentage development in one unit of time; at three equally spaced temperatures, a; $a+b$; $a+2b$.

The data obtained on the duration of the egg stage at different temperatures in *A. m. labrachiae*, *A. m. maculipennis* and *A. m. melanoon* are tabulated in Tables 1–4, and all calculations which follow have been based on the consolidated results given in Table 4. It would have been preferable to have expressed these results by expressions of the second type, i.e. formula 2 above, but it will be noticed in Table 4 that it is possible to find three nearly equally spaced temperatures only for *A. m. labranchiae* (10·6°, 17·3° and 24·3°) and not for the other two races. The time taken to complete development, and the rate of development of the eggs of *A. m. labranchiae* at different temperatures can be expressed by the following formulae:

Table 3. *Incubation periods of eggs of* A. m. melanoon *at different temperatures*

Date	Mean daily temperature ° C. Maximum	Minimum	Mean	Incubation period in days
26 February	10·7	10·3	10·5	11
4 March	11·5	9·9	10·7	12
5 ,,	11·9	9·9	10·9	13
6 ,,	12·0	9·8	10·9	12
6 ,,	12·0	9·8	10·9	12
3 April	16·0	14·2	15·1	7
14 ,,	17·4	14·8	16·1	5
17 ,,	18·1	16·1	17·1	5
18 ,,	17·9	16·5	17·2	5
19 ,,	17·9	16·5	17·2	5
28 ,,	17·4	16·0	16·7	4
29 ,,	17·0	15·6	16·3	5
29 ,,	17·3	15·9	16·6	4
30 ,,	16·6	15·2	15·9	5
4 May	17·8	14·4	16·1	5
6 ,,	19·4	15·4	17·4	4

Table 4. *Mean incubation periods of eggs of* A. m. labranchiae, A. m. maculipennis *and* A. m. melanoon *at different temperatures.*

A. maculipennis Race:	Mean temperature ° C.	Mean incubation period in days	No. of experiments
labranchiae	10·6	12·6	10
	12·15	10·0	2
	13·8	7·0	1
	14·35	5·5	4
	15·9	4·8	5
	17·3	4·2	5
	24·3	2·0	7
maculipennis	10·6	10·0	2
	11·8	8·0	2
	14·3	5·25	4
	15·2	5·0	6
	16·5	4·0	3
	21·2	3·0	4
	24·4	2·0	1
melanoon	10·8	12·0	5
	15·9	5·4	5
	17·0	4·5	6

(A) Temperature-Time (Fig. 1, A)

$$y = \frac{1 + e^{4\cdot2529 - 0\cdot1957x}}{0\cdot8192},$$

where y = incubation period in days and x = temperature ° C. (x and y are used throughout this paper to represent temperature ° C. and time in days respectively.)

(B) Temperature-Rate of Development (Fig. 1, B)

$$\frac{100}{y} = \frac{81\cdot92}{1 + e^{4\cdot2529 - 0\cdot1957x}},$$

where $100/y$ = average percentage development in one day.

The incubation periods at similar temperatures of *A. m. maculipennis* appear to be consistently lower than those of either *A. m. labranchiae* or *A. m. melanoon* (Tables 1–4).

Records have been taken of the incubation periods for the eggs of these three *A. maculipennis* races between 9·7° C. and 25·6° C. This range is not near

where x = temp. ° C.,
y = incubation period in days,
a = the mean of the values of log y,
b = the regression coefficient,
and c = mean of the values of log x.

The expressions calculated by this method are plotted in Fig. 2. They are:

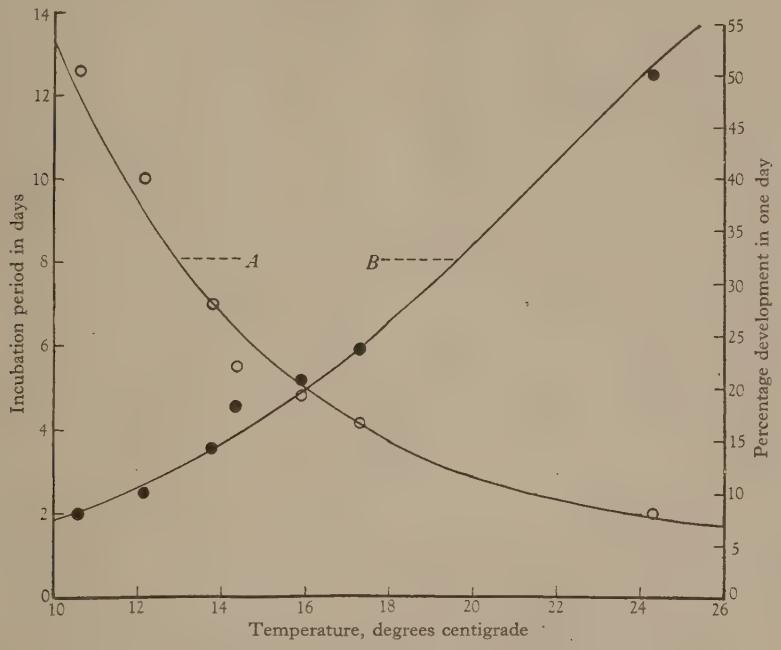

Fig. 1. (A) Temperature-Time curve of *A. m. labranchiae* eggs (open circles).

$$y = \frac{1 + e^{4\cdot2529 - 0\cdot1957x}}{0\cdot8192}.$$

(B) Temperature-Developmental Rate curve of *A. m. labranchiae* eggs (closed circles).

$$\frac{100}{y} = \frac{81\cdot92}{1 + e^{4\cdot2529 - 0\cdot1957x}},$$

x = temperature ° C. y = incubation period in days. $100/y$ = average percentage development in one day. Data from Table 4.

the critical temperatures for biological reactions and so it is permissible to represent the relationship between the time taken for the eggs to hatch at a given temperature by expressions of the type given by formula (1) above. These relationships have been obtained for each race by calculating the regression coefficient of the logarithm of the incubation period on the logarithm of the temperature ° C. and then substituting in the general expression:

$$\log y = a + b\,(\log x - c),$$

(i) *A. m. labranchiae* $\log y = \log 2522 - 2\cdot2499$ $(\pm 0\cdot11796) \log x$;
(ii) *A. m. maculipennis* $\log y = \log 736 - 1\cdot8374$ $(\pm 0\cdot08879) \log x$;
(iii) *A. m. melanoon* $\log y = \log 1906 - 2\cdot1284$ $(\pm 0\cdot08223) \log x$.

It was necessary to determine, on the basis of the data in Table 4, whether there were statistically significant differences between these expressions. To achieve this, the regression coefficients were com-

pared in pairs by the method given in Fisher (1944), para. 26.1. This comparison revealed a highly significant difference between the regression coefficients of *A. m. maculipennis* and those of the other two races. Indeed, when comparing the regression coefficients of *A. m. maculipennis* and *A. m. labranchiae* the statistic t had a calculated value of 3·50, and since there were 10 degrees of freedom ($n=10$) in this calculation the probability (P) of these coefficients

4. DISCUSSION

It appears from an analysis of the data recorded in this paper that there is a difference in the rates of egg development in the three races of *Anopheles maculipennis* studied—*A. m. maculipennis*, *A. m. labranchiae* and *A. m. melanoon*. At 10° C. eggs of *A. m. maculipennis* develop more rapidly than eggs of either *A. m. labranchiae* or *A. m. melanoon*, but as the temperature

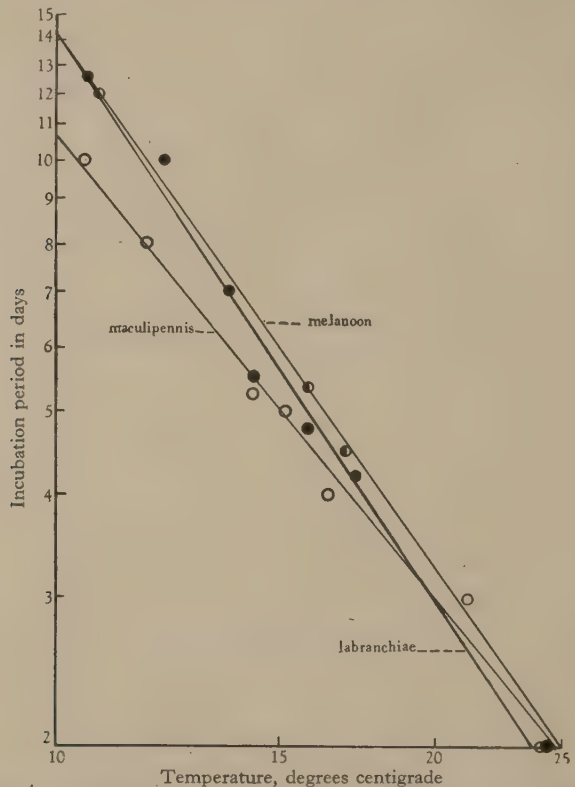

Fig. 2. Relationship between incubation period in days and temperature ° C. Logarithmic coordinates. Data from Table 4. *A. m. labranchiae* represented by closed circles. *A. m. maculipennis* represented by open circles. *A. m. melanoon* represented by half-closed circles.

having been obtained from two separate samples of the same population was less than one chance in a hundred ($P<0·01$). Similarly, the value of t calculated from a comparison of the regression coefficients of *A. m. maculipennis* and *A. m. melanoon* was 4·26 and the corresponding value of $P<0·01$. Between the regression coefficients of *A. m. labranchiae* and *A. m. melanoon* no such significant difference was revealed ($t=1·64$ and P was between 0·1 and 0·2).

is raised this difference becomes less and less until in the region of 20° C. it is negligible (Fig. 2).

It is interesting to consider whether this physiological difference is of value to these races in their natural habitats. *A. m. maculipennis* is widely distributed throughout Northern and Central Europe; to the south it occurs in Albania and Italy; in Spain it has only a very restricted distribution. In its southerly range it is more common among the inland

hills than on the coastal plains (Bates & Hackett, 1939; Lewis, 1939). *A. m. labranchiae*, on the other hand, is restricted in its distribution to the western half of the Mediterranean, where it is widespread throughout the coastal plains of Algeria, Sicily, Corsica, Sardinia and Southern Italy.

A. m. melanoon has only been recorded from northern and central Italy. In the north it is abundant on the Lombardy plain where it breeds in the rice fields around Milan. In central Italy it is particularly numerous on the west coast around Lago di Massaciuccoli (10 miles north of Pisa) and Lago di Fondi (70 miles south of Rome).

A. m. maculipennis is therefore exposed to a more rigorous climate than either *A. m. labranchiae* or *A. m. melanoon*. It shows adaptations to its colder environment particularly in the autumn when it develops a large fat body, ceases to feed, seeks a cold shelter where it remains quiescent and its ovaries do not develop. Its hibernation is an example of true diapause, since the mere elevation of its body temperature will not induce it to feed. Even with 'forced' feeding many meals are needed to mature the ovaries, whereas normally one blood meal is sufficient (La Face, 1933).

A. m. labranchiae does not hibernate so completely and is easily induced to feed and lay eggs throughout the winter. The quicker development of the eggs of *A. m. maculipennis* at lower temperatures compared with those of *A. m. labranchiae* and *A. m. melanoon* is possibly another adaptation to the colder climate experienced by this race.

5. SUMMARY

1. Wild caught female *Anopheles maculipennis* oviposited on water in small cages. Times until hatching were observed in relation to mean shade temperatures from February to June.

2. Eggs of *A. m. maculipennis* developed more rapidly than those of *A. m. labranchiae* or *A. m. melanoon*. This difference was pronounced at 10° C. but negligible at 20° C.

3. Compared with the other two races, *A. m. maculipennis* is exposed to a more rigorous climate, to which its shorter developmental period is probably adapted.

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REFERENCES

Bates, M. (1939). 'The use of salt solutions for the demonstration of physiological differences between the larvae of certain European anopheline mosquitoes.' Amer. J. Trop. Med. 19: 357–84.

Bates, M. (1940). 'The nomenclature and taxonomic status of the mosquitoes of the *Anopheles maculipennis* complex.' Ann. Ent. Soc. Amer. 33: 343–56.

Bates, M. & Hackett, L. W. (1939). 'Distinguishing characteristics of the population of *A. maculipennis* found in Southern Europe.' Verh. VII. Int. Kongr. Ent. 3: 1555–69.

Bélehrádek, J. (1926). 'Sur la formule générale exprimant l'action de la température sur les processus biologiques.' C.R. Soc. Biol. Paris, 95: 1449–52.

Davidson, J. (1944). 'On the relationship between temperature and rate of development of insects at constant temperatures.' J. Anim. Ecol. 13: 26–38.

Fisher, R. A. (1944). 'Statistical methods for research workers.' 9th ed. London.

La Face, L. (1933). 'Contributo allo studio della biologia delle diverse razze di *Anopheles maculipennis*.' Riv. Malariol. 12: 1069–114.

Lewis, D. J. (1939). 'Seasonal and geographical distribution of *Anopheles maculipennis* in Albania.' Riv. Malariol. 18: 237–48.

Mayr, E. (1942). 'Systematics and the origin of species: from the viewpoint of a zoologist.' New York.

Missiroli, A., Hackett, L. W. & Martini, E. (1933). 'Le razze di *Anopheles maculipennis* e la loro importanza nella distribuzione della malaria in alcuni regioni d'Europa.' Riv. Malariol. 12: 1–56.

Powsner, L. (1935). 'The effects of temperature on the durations of the developmental stages of *Drosophila melanogaster*.' Physiol. Zoöl. 8: 474–520.

Swellengrebel, N. H. (1929). 'La dissociation des fonctions sexuelles et nutritives (dissociation gonotrophique) d'*Anopheles maculipennis* comme cause du paludisme dans les Pays-Bas et ses rapports avec "l'infection domiciliaire".' Ann. Inst. Pasteur, 43: 1370–89.

INTERSPECIFIC COMPETITION

By A. C. CROMBIE, *From the Zoological Laboratory, Cambridge*

(With 3 Figures in the Text)

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1. INTRODUCTION

The section of Darwin's theory of natural selection concerned with the struggles for existence, as developed in the third and fourth chapters of *The Origin of Species*, contains the following argument: (1) The potential rate of increase of organisms is greater than that which the resources of the environment can support. (2) The range of physical conditions in which a given organism can survive, and the kind of matter which it can convert into the tissues of its own species (i.e. the range of conditions to which it is adapted) are limited. (3) The failure of organisms to survive or to be born may then be due to any of three agencies: (*a*) the direct action of the physical environment, e.g. climate or soil; (*b*) other organisms apart from competitors (predators, parasites, etc.); or (*c*) competition, defined as the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply (Darwin, 1859, pp. 62–3; cf. Clements & Shelford, 1939, pp. 159–60). The proportion of organisms eliminated by competition decreases with the increasing severity of the physical environment, predation, or any other agency reducing the ratio of population to resources. (4) When competition occurs it is severest between organisms with the most similar needs and habits. (5) In general, similarity in needs and habits tends to be greater the closer the taxonomic relationship. Hence (6) as new forms appear in a given locality, either by evolving there or by migration after divergence elsewhere, they will either eliminate or be eliminated by their nearest relatives if they compete with them, unless (7) each form becomes adapted to its own special habitat, when competition between them ceases in those habitats and all may survive together.

It is proposed to consider Darwin's thesis by examining, first, examples of competition between different species and varieties under both experimental and natural conditions, and secondly, differences in ecology (structure, habit) or distribution which may be attributed to competition. In most of

the examples the competing forms will not interbreed. Such breeding barriers may arise through genetic changes (e.g. polyploidy) within an interfertile group, but more often they appear to have arisen after some form of geographical or ecological isolation. The principles are exactly similar if two competing forms, e.g. mutant and wild type, do interbreed. In each case genes producing certain phenotypes are eliminated by differential survival: the study of this, as Robson & Richards (1936) emphasize, is essential to the demonstration of selection in natural populations. Interbreeding merely complicates the situation: the mutant gene is potentially able to spread through whole population and may, for instance, escape elimination by becoming recessive (see Fisher, 1930; Dobzhansky, 1941; Huxley, 1942; Mayr, 1942; and Mather 1943).

(*a*) *Factors governing population growth in general*

All organisms tend towards unlimited increase, but in this they meet resistance from their physical and biological environment (Chapman, 1931). There are thus three factors involved: (*a*) the organism itself, i.e. the range of environmental conditions to which it is adapted and characteristics such as its life-history and method of reproduction, (*b*) the physical or abiotic environment, e.g. climate and soil, and (*c*) the biological environment, comprising the effects of organism upon organism, which occur either directly, or indirectly through the reaction of organisms upon the physical environment, e.g. 'conditioning' of the medium by waste products and consuming food. The operation of biotic factors is usually density-dependent and that of abiotic factors independent of population density (Smith, 1935; Thompson, 1939). These factors may in turn stimulate, inhibit or be neutral towards the increase in density or distribution of the whole community of organisms or of certain species within it (Clements & Shelford, 1939).

Changes in population density are determined by the rates at which adults are produced and die. Such changes, i.e. the rate of population growth, are the measure of success in the struggle for existence, of which competition is a part. In organisms reproducing sexually with cross-fertilization, the upper limit of the rate of production of adults for the whole population is set by the average rate of production of male and female gametes and the sex-ratio. With self-fertilizing hermaphrodite organisms this upper limit is set simply by the rate of production of gametes, and with organisms reproducing asexually by the rate of division, budding, spore-formation, parthenogenesis, etc. Failure to reach this upper limit may be due to causes operating at any stage of the life-history. These causes fall into the three categories distinguished above. According to Clements & Shelford (1939, p. 180), who give an historical summary and an extensive review of the literature, 'there are eight causes of failure to produce a large number of later juvenile or adult offspring.... They are (1) decrease in the number of eggs produced or fertilized, owing to various causes, or destruction of eggs and very young stages; (2) death of adults and late juvenile stages from adverse physical conditions; (3) destruction by enemies and disease; (4) quantitative or qualitative insufficiency of food; (5) unsuccessful competition for space, shelter or food; (6) physiological changes in reproductive vigor; (7) initial shortage in reproducing population; (8) cannibalism. To these one may add certain assumptions such as loss of immunity, etc. but of these little is definitely known'.

The operation of the three types of causes and the relation between them have recently been discussed by a number of authors, to whose writings a general guide may usefully be given at this point. The subject has been discussed in general by Elton (1927, 1930, 1933), Chapman (1931), Prenant (1934), Bodenheimer (1938), Clements & Shelford (1939), Pearse (1939) and Severtzoff (1941); while Pearl (1925), Allee (1927, 1931, 1934), Gause (1934), Hammond (1938, 1939), Park (1938), Vevers (1938, 1939), MacLagan (1941) and D'Ancona (1942) have reviewed the literature on the operation of density-dependent factors.

Work analysing the determinants of population growth of particular organisms or from a particular point of view is reviewed by the authors given in the list which follows. Reference to further original papers is made in the 'Notices of publications on the animal ecology of the British Isles' in the *Journal of Animal Ecology*; in the reviews of ecological literature in the *Journal of Ecology*; and in the 'Current Bibliography' of the *Journal du Conseil Permanent Internationale pour l'Exploration de la Mer*; other original work is discussed in § 1 (*a*) of the present paper.

Bacteria: Buchanan & Fulmer (1928–30) and Hinshelwood (1944) on populations of bacteria and other microörganisms in the soil, Zobell (1946) on marine bacteria.

Yeast: Richards (1934) on yeast growth (with mathematical treatment), Williams (1941) on growth-promoting nutrilites for yeasts.

Fungi: Garrett (1934, 1938, 1939, 1944) on soil-borne fungi, particularly in relation to root disease.

Other plants: Clements (1916), Clements, Weaver & Hanson (1929) and Tansley (1939) on plants in general, particularly in relation to ecological succession.

Protozoa: Jahn (1934), Johnson (1937, 1941), Allee (1941), Hall (1941 a), and Richards (1941) on

the growth of protozoan populations with particular reference to density-dependent factors, Taliaferro (1941) on blood-dwelling species, Hall (1941*b*) on food requirements; Hall & Shottenfeld (1941) on density and population growth of *Glaucoma piriformis*.

Rotifera: Edmondson (1944, 1945).

Crustacea: Gause (1932) on population growth, Berg (1934) and Banta (1937) on population density and sex-determination in Cladocera; Wilder (1940) on density and population growth of the amphipod *Hyalella azteca*.

Insects: *General.* Chapman (1939), Imms (1937) and Voûte (1943) on population growth in general, Uvarov (1931) and Gause (1932) on the influence of the physical environment, Graham (1939) on forest insects, King (1939) on soil insects, Carpenter (1940) on insect outbreaks.

Parasites, fluctuations and biological control: Smith (1939), Thompson (1939) and Clausen (1940) on the subject in general, Nicholson & Bailey (1935) and Smith (1935) on mathematical treatment, Flanders (1939, 1942) on the control of the sex-ratio and of oviposition, respectively.

Social insects: Bodenheimer (1937*a*, *b*), Emerson (1939*a*, *b*).

Experimental populations: Ford (1937), Park (1937, 1941, 1942), Crombie (1944*a*, 1945, 1946); Robertson & Sang (1944*a*, *b*) on population growth of *Drosophila*.

Marine life: Lucas (1938) on plankton, Harvey (1942) on the production of plant life in the sea, Russell (1942) on fish, Burkenroad (1946) on starfish, Zobell (1946) on marine bacteria.

Mammals and Birds: Severtzoff (1934, 1941) and Elton (1930, 1942) on population growth, Kendeigh (1944) on the measurement of bird populations, Hammond (1941) on fertility.

Man: Carr-Saunders (1922) and Hogben (1931) on the biological aspects, Carr-Saunders (1936) and W. S. Thompson (1942) on the social aspects, and Kuczynski (1935) on the measurement of population growth. On the history of human population theory: Malthus (1798), Strangeland (1904), Bonar (1931).

Comparative mortality: Pearl (1922), Pearl & Miner (1935), Davis (1945).

Outbreaks and sunspot cycles: Clements & Shelford (1939), MacLagan (1941).

Fluctuations of predator and prey, and epidemics: Gause (1934, 1935), Volterra & D'Ancona (1935), D'Ancona (1942); Topley (1926, 1942) and Greenwood *et al.* (1936) on experimental epidemics.

Mathematical treatment of population growth and competition: Lotka (1925, 1934, 1939, 1945), Gray (1929), Gause (1934, 1935), Volterra & D'Ancona (1935), Kostitzin (1937), D'Ancona (1942), D'Arcy W. Thompson (1942); other references in Crombie (1945, 1946); Leslie (1945) on the use of matrices.

(*b*) *Factors tending to reduce competition*

Only density-dependent factors are directly involved in competition although density-independent factors may, through the competing organism's intrinsic nature (e.g. adaptation to different environmental conditions), determine the outcome of competition and also whether it occurs at all. Competition is reduced by factors which keep the ratio of population to environmental resources low and increased by those which produce the reverse effect. Such factors may be classified under three headings.

(1) *The organism itself*

(*a*) The mortality which occurs at different stages of the life-history as a result of competition will vary from organism to organism according to its method of reproduction. If the adults continue to reproduce regardless of the resources available, competition will occur and supernumerary individuals be eliminated in either the juvenile or adult stages. If the adults limit their rate of reproduction, e.g. by less frequent union between the sexes, special control exerted by the female over her rate of oviposition, or by the control of the number of reproductive individuals such as occurs in ants, bees or termites, mortality will be reduced. Elton (1927, pp. 123–5) points out that animals near the predator end of food-chains tend to have special means of regulating their numbers, e.g. by a very low rate of reproduction or the habit of having nesting territories. According to Lack (1946), bird predators of the lemming and other rodents have, besides emigration, another uncommon adaptation to the huge fluctuations of their prey. When prey is very abundant they often raise two broods a year instead of one and have clutches of up to double the size, while when their prey is very scarce they do not attempt to breed.

Control of the reproductive rate may be a response to population density. When the rate of oviposition or birth of young is regulated by competition for space among adult animals the ratio of offspring to food supply will be lower and so a higher proportion of those born will survive. Lack (1943, ch. 8) considers that the territorial behaviour of birds is unlikely to limit population in this way, but the question is one which should be examined with reference not only to birds but to other animals which possess territories (cf. Bodenheimer, 1938; Clements & Shelford, 1939; Dobzhansky, 1941, p. 170; Elson, 1942). Competition for space which limits population, although relatively unimportant compared with other factors, occurs in insects which compete for definite oviposition sites, e.g. the weevil *Sitophilus oryzae* (MacLagan, 1932; MacLagan & Dunn,

1935), the beetle *Rhizopertha dominica* and other insects (Crombie, 1942, 1943). Competition for mates which reduces the frequency of mating would have the same effect (cf. MacLagan & Dunn, 1935; Reynolds, 1944; Flanders, 1945).

References to control of oviposition depending on the presence and quantity of suitable larval food and sites for development are given by Russell (1941). Striking examples of this are to be found among entomophagous insect parasites in which, like many other Endopterygota, adults and young occupy different environments (Clausen, 1940). The adult female must first be able to find the hosts on which her larvae feed. The rate at which this occurs is determined not only by host density, but by the skill shown by the parasite in her search (cf. Thorpe & Caudle, 1938; Laing, 1937, 1938; Varley, 1941; Wilkes, 1942). As de Bach & Smith (1941*a*) point out, such skill is a specific characteristic. The rate of oviposition depends upon this and two other processes: oögenesis whereby eggs are produced, and oviposition whereby, in response to a group of stimuli which would be normally obtained only from the appropriate host, eggs are laid. According to Flanders (1942), in some Parasitic Hymenoptera, oögenesis does not occur unless the female is able to feed on the host appropriate to its larvae. When conditions are favourable to oviposition, the number of eggs which each species places on each individual host is fairly constant and largely independent of host density. This is achieved on the one hand by the females having a ready supply of eggs available when hosts are found, and on the other, when suitable hosts are few, by their ability both to discriminate between parasitized and unparasitized specimens and to exercise restraint from oviposition in the former (cf. Salt, 1934, 1937; Ullyett, 1936; Jacobi, 1939; Lloyd, 1939, 1940). By such restraint they are able to prevent mortality in the immature stages through overcrowding. The maintenance of reproductive capacity when environmental contions are unsuitable for oviposition, and the ability to restrain from oviposition, which is essential to host selection, are made possible by two adaptations. Some species store ripe eggs. Others have eggs which cannot be stored longer than the incubation period. In them oösorption sets in and proceeds at the same rate as oögenesis until conditions suitable for oviposition once more arise.

(*b*) Changes in the organism itself may occur which alter the existing relationship between biotic potential and environmental resistance or cause organisms of different species to cease to interfere with each other and so affect competition. Some changes of this kind are at present not always referable to causes outside the organism itself, e.g. genetic mutations and changes in physiological vigour, such as the changes in reproductive rate and viability of insects and other animals and in the resistance of the host-plant or animal noted by Clements & Shelford (1939), Carpenter (1940) and Shelford & Flint (1943). Others are known to be responses to the environment, but are independent of population density, e.g. changes in response in given aspects of the environment such as those brought about by 'olfactory conditioning' in insects (Thorpe, 1930, 1940; Crombie, 1944*b*) and other forms of learning (Thorpe, 1943*a*, *b*, 1944*a*, *b*) which may enable an animal to make use of a new food or habitat. Others are brought about by competition itself, e.g. changes in size, sex-ratio, reproduction, rate of development and longevity, and changes in morphology and behaviour as in aphids and locusts (Allee, 1931, 1934; Hammond, 1938, 1939) and in the insect parasites described by Salt (1941). An example of dwarfing due to crowding in plants is described by Mason (1915) in his work on the lodgepole pine. Two important examples of changes of this kind are the 'adaptation' undergone by plants (§2(*b*)) and the observation by Shelford (1911), in his study of ecological succession in fish, that the succession of species is the result of the stability of the *mores* (physiology, behaviour, habits and mode of life). When *mores* are flexible, species do not succeed one another when changes occur in the environment, but the same species remain there with changes in behaviour and physiological characters.

(2) *The physical environment*

This may reduce competition in two ways: (*a*) It may cause an increase in food or other resources fast enough to allow a rapid increase in populations of the competitors. Elton (1930), Clements & Shelford (1939) and Timoféeff-Ressovsky (1940) have drawn attention to the importance of this and it is sufficiently obvious in the dependence of many population changes upon climate and weather (e.g. Rivnay, 1938; Andrewartha, 1944; and Ribbands, 1944 on insects; Cross, 1940 on mammals). But environmental resources cannot go on increasing for ever and a time must come when competition will occur, unless prevented by something else. (*b*) It may adversely affect the competitors, but not their food, living space, etc., so that the ratio of population to resources remains low. This occurs in unfavourable habitats such as deserts and high mountains where among plants there are 'open communities' (Tansley, 1939), and may also affect lichens on rocks and the inhabitants of swiftly moving streams. As Darwin points out: 'On the confines of its geographical range, a change of constitution with respect to climate would clearly be an advantage to our plant; but we have reason to believe that only a few plants or animals range so far, that they are destroyed

by the rigour of the climate alone. Not until we reach the extreme confines of life, in the Arctic regions or on the borders of an utter desert, will competition cease' (1859, p. 78). It is there too that the most violent fluctuations in numbers and also migratory movements are likely to occur (Huntington, 1931; Carpenter, 1940). Under exceptional circumstances a density-independent physical factor may allow organisms exactly to replace themselves from generation to generation. But except for this very improbable case, if the organisms survive at all in its presence, such a factor could not itself limit population growth and suspend competition more than temporarily. Either the organisms will not be viable in its presence, or if they are they will increase until they compete for something, e.g. if not for food then for space—as in swiftly running streams where there may be competition for lodging sites, and this will limit population density.

(3) *The biological environment*

One organism may reduce the competition occurring between members of another species (or between two other different species) in a number of different ways: (*a*) Being the food of the latter it may increase rapidly. In a finite world the increase of the food will eventually reach a limit, but while its rate of increase is greater than that of the organisms feeding on it, i.e. while 'temporarily super-abundant' (Lack, 1946), there will be no competition between the latter. A situation in which competition is temporarily reduced, if not prevented, is exemplified by the changes in populations of predators or parasites which follow those of their prey or hosts, e.g. Cutler & Crump (1920) and Cutler, Crump & Sandon (1922) on fluctuations of soil bacteria and Protozoa; de Bach & Smith (1941*b*) on fluctuations of insect hosts and parasites; Huntsman (1941) on fish and birds; and Crombie (1944*c*) on rats and cats. (*b*) It may prey on or parasitize the competitors. In his discussion of optimum population density Elton (1930) points out that without predators to control its numbers an organism is in danger of increasing above the population the food supply can support. This seems to have happened to the Kaibab deer (Rasmussen, 1941). Fuller (1934) points out that competition among fly larvae attacking carcasses is relieved by the parasitism of Hymenoptera (cf. Brues, 1923). Similar examples are given by Severtzoff (1934), Clements & Shelford (1939) and Errington (1946). But agencies such as predators may produce a different kind of competition rather than preventing it altogether. They may, for instance, prevent competition for food among their hosts, but cause them to compete to avoid the predators, e.g. there may be selection for reflexes which assist this. (*c*) An organism may suppress all the competitors by more powerful competition for the resources for which they compete, perhaps leaving them to survive in separate niches for which they do not compete with each other. (*d*) It may react upon the environment so as to affect the conditions of competition. The third and fourth effects are brought about especially by ecological dominants which may reduce competition among subordinate forms. There is probably little intraspecific competition among the subordinate insects in the sewage beds described in §2(*e*) or among the less successful species of granivorous insects of which a small population manages to survive in special niches in a medium dominated by its more powerful competitor. A similar effect upon subordinates may be brought about by reaction upon the environment. This is more characteristic of some plant dominants (§2(*b*)). An example from animals is given by Cahn (1929), who claimed that carp introduced into a lake transformed the bottom vegetation and other aspects of the environment so that the other species of fish were reduced to very small numbers.

(*c*) *Consequences of interspecific competition*

Competition occurs between species with similar needs and habits when the ratio of their population to environmental resources reaches a certain value. This ratio may be kept low and competition prevented by the various agencies discussed above. When competition does occur external factors may change at intervals (e.g. seasonally), alternately favouring one then the other of two competitors, so that first one tends to increase at the expense of the other and then the latter at the expense of the first. Such a situation would produce forced fluctuations in populations of the two species. But if external conditions (other than those brought about by the organisms themselves, for these are part of the process of competition) remain constant enough not to reverse their competitive relationship in this way, it may be demonstrated by a simple argument that two species with *identical* needs and habits cannot survive in the same place if they compete for limited resources—at least not if their needs and habits remain identical. The same conclusion applies to organisms with *similar* rather than identical ecology, but the necessary degree of similarity can only be discovered empirically. This conclusion is explicit in *The Origin of Species* (Darwin, 1859, pp. 75, 110–15) and the biological consequences of this situation have recently been developed by Gause (1934) (see also Lotka, 1925; Volterra, 1926; Kostitzin, 1937; Volterra & D'Ancona, 1935; D'Ancona, 1942).

Now the superiority of one species over another must be estimated in terms of the whole life-cycle,

and must include adaptability as well as adaptation (§2(*c*)). Individuals of one species may then be superior to those of another in two different ways: (*a*) in the combined *rate of reproduction and survival* independent of interspecific interference: this will depend on adaptation to the environment, or (*b*) in *interference* (through direct attacks, conditioning the medium, consuming food, etc.) which reduces the rate of reproduction and survival of the competitor. A superior rate of reproduction and survival of course affects the competing species through interference: if there were no interference, there would be no competition. But the two modes of superiority are distinct (de Candolle, 1820; Lyell, 1830–33; Darwin, 1859, p. 69).

Let x and y be two species with identical needs and habits competing for the same resources of a limited environment. There are two cases:

(1) Suppose x to be superior to y in interference, but equal in rate of reproduction and survival. Then if at some time the two species have equal populations, each will reduce the succeeding generation of the other, but x will reduce y's proportionately more than y reduces x's. The advantage of x over y is a property of each individual, so that the total advantage of the population of x over that of y will depend on the number of individuals of each species present. x will then form more and y less than half the total population, and its relative advantage over y will therefore have increased. This will lead to a still greater relative increase of x in the second generation, which, in turn, will give it an even greater relative advantage over y, and so on, since there is nothing to make y approach a limit other than zero, until the latter is entirely eliminated from the ecological niches for which it competes with x. It may of course survive in niches in which it is superior to or does not compete with x. If y began with a sufficient numerical superiority, the advantage would then go to this species and it would eliminate x, the critical numerical superiority required depending on the 'amount of advantage' of an individual x over an individual y and on the exact conditions of the struggle.

(2) Now let the interference of each species with the reproduction and survival of the other be equal, and let x have a higher rate of reproduction and survival than y. The total number of individuals which a limited environment can support is limited. Let the number of x and y be equal at some time when the total population is approaching its limit. Owing to lack of food, space, etc. in the first generation after that, each species will lose a proportion of its numbers, the proportions being equal since the interference of each species with the other is equal. But as x increases faster than y it will now represent more than half the total population. In the second generation the proportions of their numbers lost by the two species will again be equal, but the absolute numbers of x will again be relatively greater; and so on until x alone remains. As before, if y began with a sufficient numerical superiority, the critical value of which depends on the relative rates of reproduction and survival of the two species, it would in the same way be able to eliminate x.

It is conceivable that the advantages of two species derived from the rate of reproduction and survival, interference and numbers may at some time be precisely balanced. But since the balance would depend on numbers as well as on the other factors, and since in nature numbers are subject to fluctuations caused by environmental changes, such a balance would be highly unstable. It follows, then, that if the conditions enumerated above which allow competition are fulfilled, two species with identical needs and habits will not survive together in the same limited environment. By a similar argument Nicholson & Bailey (1935, p. 582) have shown that when two or more host-species are attacked by a common parasite-species only one host is likely to survive. A corollary to this theoretical conclusion, which seems inescapable, is that if in nature such species are found together, then either one or more of the necessary conditions must be lacking, or the species must differ in their ecology.

One special point seems worth mentioning here. If two competing species meet along an environmental gradient each end of which favours one of them, there would theoretically be a certain point on the gradient on either side of which each would be superior to the other (cf. Gause & Witt, 1935). Each would then exclude the other from its favoured area and the boundary between them would be sharp. Examples of this situation are given in §2 (e.g. Beauchamp & Ullyott, 1932; Gause, 1936). But in nature where environmental conditions fluctuate this boundary would be continually moving, describing an area in which the two species would be in a state of unstable overlap (Lack, 1945). Finally, while the argument applies to monophagous and polyphagous species with the same food and habits, Lack (1946) has drawn attention to the complexity of competition between polyphagous species with slightly different food preferences and the importance of the time factor. For instance, two species which compete for common food most of the time may survive together because of the occurrence, at intervals shorter than the time it takes for one species to eliminate the other, of periods of temporary abundance of a second food to which one of the competitors transfers its complete attention, during which periods each species is able to re-establish its numbers without interference from the other. Such examples serve to remind us of the complexity of the interrelationships between organisms in nature.

2. INTERSPECIFIC COMPETITION IN EXPERIMENTAL CULTURES AND IN THE FIELD

The factors controlling population growth and the ecological relations between competing species have been accurately determined in only a limited number of cases. Only when this has been done can the operation of the theoretical conclusions reached in § 1 be examined. But for the assistance of others proposing to study this subject reference will be made below to all the important work known to the author dealing with interspecific competition. Only a very summary analysis has been made of non-zoological literature.

(*a*) *Plant microörganisms*

Interactions between plant microörganisms in general have been reviewed by Fawcett (1931), Nicol (1934), Russell (1937), Waksman (1937) and Garrard & Lockhead (1938); while Holman (1928) and Buchanan & Fulmer (1930) have paid particular attention to bacteria in their hosts and in artificial media (cf. Régnier & Lambin, 1934). White, Robinson & Barnes (1938) describe 'transformations' in pneumococci which may involve selection between different biotypes. Garret (1934, 1938, 1939), Porter & Carter (1938), Weindling (1938) and D'Aeth (1939) review interactions between fungi in the soil, the host plant and in artificial media (cf. Lal, 1939).

Many types of interaction occur between plant microörganisms, from reciprocal symbiosis or stimulation of reproduction to antagonism involving inhibition or destruction. There are three main explanations of these phenomena: competition for energy materials and nutrients or synergetic effects in which the metabolic products of one organism form a suitable source of energy and food for the other; changes in the environmental conditions of the substrate, e.g. in *p*H or oxidation-reduction potential, brought about by one of the organisms; and the formation of specific substances (enzymes, toxins, stimulants) which directly affect the other organism. Among soil fungi some saphrophytes actually attack and assimulate the mycelium, etc. of other parasitic forms (Garrett, 1939). These complicated interactions lead to a state of mutual equilibrium between the populations of microörganisms in the soil. The modification of this, e.g. by the increase of one group of organisms, leads to the depression of others, e.g. near competitors. Environmental conditions, e.g. temperature, *p*H, moisture, aeration and the presence of specific nutrients, often have a selective effect enabling the organism which they suit best to develop more rapidly and suppress the others. Environmental conditions may affect the production of toxins as well as the growth of an organism and competition for the same food supply.

Among fungi, according to D'Aeth (1939), two organisms may grow together in the same place in the host plant and develop independently as long as their spheres of physiological activity do not overlap. Nicol & Thornton (1941) worked on competition between related strains of nodule bacteria and its influence on infection of the legume host. When two strains are both present in the surroundings of their host root system, active competition between them may cause the strain having the higher initial growth-rate almost completely to check the multiplication of the other strain outside the plant. This dominant strain will then be responsible for nearly all the nodules. 'This competition can be compared with the intraspecific selection that takes place in higher organisms and may well be more acute than competition between more distantly related microörganisms whose environmental requirements are more dissimilar.'

Gause (1934) studied the competition in an artificial media between two yeasts belonging to different genera. Beginning with small inocula the growth of each was inhibited under aerobic conditions by the ethyl alcohol produced, and under anaerobic conditions by this and probably other metabolic waste products. Growth ceased before the food supply was exhausted and both kinds still existed together when the experiment ceased. As the exact chemical constitution of the media is unknown it is impossible to say to what extent they competed for the same nutrients, although Gause (1935, Table 2) seems to assume that one would have eliminated the other (the victor depending on the conditions) had the experiment continued.

(*b*) *Higher plants*

The large literature on competition in plants has been reviewed by Warming & Vähl (1909), Clements (1916), Clements, Weaver & Hanson (1929), Salisbury (1929, 1940) and Braun-Blanquet (1932), while additional work is discussed by Gause (1934, 1936), Cain (1939), Carpenter (1939), Clements & Shelford (1939), Tansley (1939), Diver (1940), Dobzhansky (1941), and Huxley (1942). Stapledon & Davies (1928) and Davies (1928) describe competition between species in seed mixtures; Bystrikov (1931) competition between various cultivated plants; Eisele & Aikman (1933) competition in pastures; and Pavlychenko & Harrington (1934) the competitive efficiency of weeds and cereal crops. Only the briefest statement of general conclusions will be given here.

According to Clements, Weaver & Hanson (1929, pp. 316 et seq.), who give a complete survey of the field and an account of their own extensive experiments: 'Competition is purely a physical process.

With few exceptions, such as the crowding up of tuberous plants when grown too closely, an actual struggle between competing plants never occurs. Competition arises from the reaction of one plant upon the physical factors about it and the effect of these modified factors upon its competitors. In the exact sense, two plants, no matter how close, do not compete with each other as long as the water-content, the nutrient material, the light and heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins.' 'As a figure of speed, competition for space is probably not objectionable, but it must not be overlooked that space really stands for the raw materials, energy and working factors that it contains.' 'Water stands first, light next, and nutrients last in native communities, with the order of light and nutrients reversed in the case of many intensive field crops. The general and probably universal rule is that the factor present in the smallest amount relative to the demand will be paramount' (see Rübel, 1935). The relations between all parts and processes of different plants may affect the competition between them. Competition seems to be constant between certain members of a closed plant community, both between individuals of the same and those of different species. In seral communities new plants are always entering and competing with those already there, and this leads to the succession characteristic of such communities. The final result is the dominance of species (usually the tallest) with the controlling reaction on water, light or nutrients and subordination of the rest. The number of dominant species is usually small, occasionally only one, even in such communities as West African tropical forests where the diversity and number of species in the community is great (Aubréville, 1938, pp. 125 et seq.), but this is unusual among tropical forests as a class. As dominance increases and unsuccessful species are eliminated competition decreases, e.g. in a climax forest there is probably little competition between the trees and the ground layer of herbs. But even in climax communities, owing to the seasonal production of new shoots and seedlings and the continuous variation of physical factors, competition still occurs, e.g. between the associated individuals of both dominant and subordinate species and between adults of the latter and seedlings of the former. Such competition 'serves to keep the composition of the population and the structure of the community substantially constant, the various classes of members being in approximate equilibrium with one another, and the community as a whole with its habitat. Thus competition between the members for light or for water maintains the community in a stable condition, preventing any one species from breaking away from its existing status in the community—as it may do if other members of the community are removed—and fresh species do not normally enter a climax community' (Tansley, 1939, p. 227).

According to Clements, Weaver & Hanson (1929), competition within a single species is keenest when individuals are most similar. With plants of different species the closeness of competition varies directly as their likeness in vegetation or habitat form, and is independent of their phylogenetic relationship except in so far as this is based upon life-form or habitat-form. This principle is of primary importance in the competition that arises between occupants and invaders in the different stages of ecological succession. A plant similar to those in a community is excluded, but 'the species so unlike the occupants that they enter at a clear advantage or disadvantage, establish themselves readily, in one case as a result of the reaction, in the other by taking a subordinate position' (Clements, Weaver & Hanson, 1929, p. 21). Competition may be avoided by separation in time (season of growth or reproduction) as well as space (height, position of shoot and root). Subordinate species in a community survive when they differ sufficiently from others or when they undergo adaptation, i.e. the adjustment of functions with consequent modifications of structure and form in response to physical factors modified by the reaction of competitors. Such functional changes involve 'absorption and root pressure, conduction, stomatal movement, transpiration and starch-content, as well as other features such as turgidity, osmotic concentration etc.' (Clements, Weaver & Hanson, 1929, p. 322). The extinction of one most often occurs when two species are similar in life-form, especially when one enjoys a marked advantage in the reaction upon light or water-content. The species which arrives first is often able by its numbers of well-rooted and reproducing individuals to suppress new-comers. Other points favouring success are duration and perennation, rate of growth (root and shoot), rate and amount of germination and vigour and hardiness especially under adverse conditions. Occasionally one species suppresses another by toxic products: thus the refuse of bracken (*Pteridium*) is injurious to some of its competitors and prevents their growth (Jeffreys, 1917; Farrow, 1925). Sometimes competition keeps plants within a narrower ecological range than they can tolerate (Salisbury, 1929). For instance, many maritime plants grow as luxuriantly or even more luxuriantly in garden soil than in their natural habitats, and their absence inland is presumably to be attributed to intolerance of competition. With pairs of calciphile and calciphobe species or different ecotypes (Tansley, 1917; Stapledon, 1928; Turrill, 1931, 1940), each is successful in its own habitat and is suppressed in and eventually eliminated from that

of the other. According to Braun-Blanquet (1932, pp. 15–16), however, the role of competition has here been frequently over-emphasized, since in many cases the basiphilous species could not survive in the habitat of the acidiphilous species and vice versa, even without competition. Sometimes the success or failure of competing species is influenced by their susceptibility to factors such as animal grazing. This is illustrated by the effect of rabbits on the vegetation of the Breckland (Farrow, 1925).

Competition is severest and 'as the final term of suppression (extinction), is most in evidence between similar life-forms' (Clements, Weaver & Hanson, 1929, p. 321). In many of the experiments described by these authors, competition between two species with similar ecology resulted in the elimination of one of them, and the results suggest that had they been continued long enough the same would have occurred in all of them. But such puzzling cases as that described by Diver (1940) are common in botanical observation. The two species of rush, *Juncus conglomeratus* and *J. effusus*, are so closely related that they were formerly regarded as two forms of one species *J. communis*. The differences between these are apparently small although definite, but the former has the narrower range of tolerance and rarely occurs alone. Where they occur together, 'so closely may they intermingle that on one occasion it was necessary to dig up a tuft to demonstrate (to a botanist) that the two species were not growing from the same root stock'. It is true that sessile habit and long life may defer the outcome of competition in plants so that observations over many years may be necessary to decide whether one species will be eliminated. But it is clear that the theoretical problem raised in § 1 suggests the need for intensive ecological studies from this point of view.

(*c*) *Protozoa*

(1) *Cultures*. Gause (1934, 1935) describes experiments carried out to study the competition between two or more species of Protozoa living on the same food. In some cases they occupied the same ecological niche and in others different ecological niches. Summaries of this work are given by Gause (1937) and Richards (1941).

Paramoecium caudatum and *Stylonychia mytilus* were grown separately and in mixed cultures in an oatmeal infusion inoculated with *Bacillus subtilis*. Each species depressed the population growth of the other as compared with growth in pure cultures, but *Stylonychia mytilus* depressed *Paramoecium caudatum* very much more than the latter did the former. With a denser oatmeal infusion sown with various wild bacteria the positions of the two species were reversed. *P. caudatum* reached the same population as when living alone. *Stylonychia mytilus* reached about half this value and then declined, but was not eliminated completely. As the exact conditions in the medium are unknown it is impossible to tell for what parts of the environment competition occurred.

When competing in a regularly renewed (unconditioned) medium containing *Bacillus pyocyaneus* as food, *Paramoecium aurelia* has two advantages over *P. caudatum*: the rate of geometric increase of the biomass of the former species is higher (1·1244 as compared with 0·794) and it accumulates a greater biomass (1·64 times) than *P. caudatum* at the expense of the same amount of food. In mixed cultures the two species increased unaffected by the presence of the other for the first few days, until the population had reached the maximum which the limited but constant amount of food could support. Up to this time each species was seizing the still unused resources of energy. Thereafter *P. aurelia* increased to the same population as when living alone and *P. caudatum* decreased to zero population. During this period there was a redistribution of completely seized energy between the two species. The reason for the lower rate of increase of *P. caudatum* in this medium is that it is more sensitive than *P. aurelia* to the waste products of the pathogenic bacterium *Bacillus pyocyaneus*. With yeast and a less virulent strain of this bacterium as food, *Paramoecium caudatum* had the higher rate of geometric increase of the two species and was more successful in competition. *P. caudatum* is also more sensitive than its rival to their own waste products. When the medium (without the virulent bacterium) containing the mixed culture was unrenewed, the initial rate of increase of *P. caudatum* was higher, but *P. aurelia* lived twice as long on the limited food present. With yeast as food *P. aurelia* had a lower rate of geometric increase than *Glaucoma scintillans* ($b = 4{\cdot}625$) and was driven out by it. In mixed populations of either *Paramoecium aurelia* or *P. caudatum* with *Stylonychia pustulata* (with *Bacillus pyocyaneus* as food) the latter protozoan was always driven out, apparently because of its sensitivity to the waste products of the bacteria.

In a renewed medium containing yeast as food *Paramoecium aurelia* and *P. bursaria* were able to survive together in a mixed culture because the former feeds in the suspension in the upper layers of liquid while the latter feeds on the bottom. The populations of the two species reached the same position of equilibrium irrespective of initial concentrations except when the initial superiority of *P. bursaria* over *P. aurelia* surpassed a certain limit. *P. caudatum* and *P. bursaria* were also able to survive in a mixed culture in a renewed medium containing both yeast and bacteria as food, because the latter feeds on the yeast on the bottom and the former on the bacteria suspended in the upper layers of liquid (cf. Singh, 1942). Again the same equilibrium position

was reached regardless of initial concentrations except when *P. caudatum* began with too great an initial inferiority, when its sensitivity to the waste products of *P. bursaria* prevented its further increase. In these experiments under controlled conditions it proved true that two competing species cannot survive together in the same place if they have the same needs and habits, i.e. occupy the same ecological niche. Gause (1934, 1935) found that the Lotka-Volterra equations gave at least a qualitative description of the changes in biomass of the two species. These equations will be discussed in a later section. Gause & Witt (1935) adapted the equations to cover the case of the 'special zone' described above where the equilibrium position was not returned to when one species began with too great an inferiority. This is of obvious importance in nature, e.g. in the establishment of plants.

Gause (1936) describes an experiment designed to study the effect of a gradual change in an external physical factor (*p*H) on the competition between two species. Above a certain value of *p*H one was successful and below this the other. The change in population at different *p*H values was sometimes physiological and independent of competition, and sometimes entirely due to the competition of a rival better adapted to the particular *p*H value. The mathematics of such a change in competitive ability in response to a gradual environmental change are discussed by Gause & Witt (1935). In an article on the relation of phenotypic adaptability to genotypic adaptation Gause (1942) describes competition, in cultures of *Paramoecium* of various species, between clones of two mating types (between which there is no conjugation). In the case of adaptation of *P. caudatum* and of *P. aurelia* to the increasing salinity of the medium, the larger part of the total adaptation is due to adaptability. The clones that survived in mixed cultures are here weak in initial strength but powerfully adaptable. On the other hand, in the case of acclimatization of *P. caudatum* to dilute solutions of quinine, adaptability is low as compared with the inherent diversity of various clones in initial resistance. The survivors here are well adapted but poorly adaptable. The different clones of the same species occupied identical niches in which only one was able to survive.

(2) *Field observations.* Interspecific competition enters into the process of succession of Protozoa in natural populations. Woodruff (1912, 1914) believed that in hay infusions the sequence of dominant species is determined by the rate of increase and the effect of specific excretory products. Gause (1936), in a review of the 'principles of biocoenology', describes the formation of protozoan climaxes in glass plates submerged in natural waters. There is an initial period when all the chief components of the community increase, followed by a period of reconstruction when competition eliminates some of the species and leaves a stable population of dominants occupying the principal ecological niches. In nature, according to Hutchinson (1941), the primary requirements of non-flagellate groups of Protozoa are light, heat and nutrient elements. The autotropic forms live under conditions of competition for nutrient substances. Very few divisions are needed to raise a species to a dominant position. Different minimal concentrations of different elements required for the maximum division rate would probably be found in different species. This provides a mechanism for succession during the period of nutrient exhaustion after a maximum for any species, for as the concentration falls the species responsible for the depletion, which dominates the initial nutrient level, will suffer from competition from other forms which are dominant at low nutrient levels. Interactions between Protozoa and other organisms in the soil are mentioned by Russell (1937) and Waksman (1937).

(*d*) *Invertebrates other than Protozoa and insects.*

Beauchamp & Ullyott (1932) studied competition between different species of freshwater triclad flatworms (Platyhelminthes) in mountain streams, and found that mutual competition restricts certain species to a narrower habitat than that in which each is capable of living when competitors are absent. When *Planaria montenegrina* and *P. gonocephela* occur in competition with each other, temperature is the factor which governs their relative success, the former dominating in parts of the stream of which the temperature is below 13–14° C. and the latter in (lower) regions where the temperature is above this value. This is an example of a gradually changing physical factor causing a sudden change in competition relations between two species and the equilibrium position reached by their populations. When *Planaria alpina* competes with *Polycelis cornuta* the chief governing factor is rate of flow of the water, the former preferring rheocrene (stream) and the latter limnocrene (pool) conditions. Temperature also affects the competition between these two species, *Planaria alpina* preferring the colder temperatures. But when limnocrene conditions extend up to the spring head into the preferred temperature the latter species, *Polycelis cornuta* either replaces or exists together with it right up to this point. Beauchamp (1932) studied the influence of ecological factors on the competition between stream and lake-living triclads. Stream forms are sometimes washed down and are capable of colonizing stony areas. *Planaria alpina* is confined to the 'Brandungszone' because among other reasons it there avoids the competition of *Polycelis nigra* with which it cannot live in close competition and which probably devours it.

According to Elton (1927, pp. 36–8) the copepod crustacean *Eurytemora lacinulata* cannot live together with another copepod *Diaptomus gracilis* in the same ponds, although it may be found in similar and neighbouring ponds from which *D. gracilis* is absent. Gause (1934, p. 22) quotes observations by Kessler and by Birstein and Vinogradov on the extermination of the broad-legged crayfish *Potamobius astacus* by the long-legged *P. leptodactylus* when the latter were introduced into lakes naturally inhabited by the former. Wilson (1917: quoted from Pearse, 1939, p. 522) states that lernaepodid crustaceans and the glochidia of clams are, as a rule, mutually exclusive when parasitizing fishes, but that a light infestation with one parasite may not be sufficient to keep off the other. On the other hand, commensals which do not compete may often occur together on the same 'host' (Pearse, 1939, pp. 504 et seq.).

(*e*) *Insects*

(1) *Cultures of granivorous insects.* The competition occurring at all stages of the life cycle between different species of granivorous insects has been analysed in detail (Crombie, 1942, 1943, 1944*a*, 1945, 1946). Several features led to the choice of these organisms for such an investigation. Their biology was already known with reasonable accuracy. A number of different species inhabit the same environment and are thus suitable for studies in interspecific competition. They breed rapidly and adults and juvenile stages live on the same food. Their food supply is easily regulated and the physical conditions of their environment kept constant. Finally, changes wrought in the medium by the organisms themselves are comparatively easily controlled. The species chosen were three beetles, *Rhizopertha dominica* (Bostrichidae) *Tribolium confusum* (Tenebrionidae) and *Oryzaephilus* (*Silvanus*) *surinamensis* (Cucujidae) and one moth, *Sitotroga cerealella* (Gelechiidae). The adults of the beetles live for several months, a period several times longer than the generation time, and following copulation the females oviposit fertile eggs more or less continuously during most of their adult lives. Male and female longevities are approximately equal. Both adults and larvae of *Tribolium confusum* and *Oryzaephilus surinamensis* feed in the open medium, e.g. crushed wheat or flour, but pupation tends to occur in crevices. The adults of *Rhizopertha dominica* feed in the open medium, but the larvae bore into wheat grains or other food materials (through crevices in which they can get the necessary leverage) and complete their development inside. The adults of *Sitotroga cerealella* live for only a few days or weeks, a period shorter than the generation time. Upon copulation, the females lay nearly all their eggs within a few days. The habits of the larvae are very similar to those of *Rhizopertha dominica*.

In insects, fecundity determines the upper limit of natality, defined as the rate of emergence of adults. But this is seldom achieved. Infertility in the eggs, and mortality in the egg, larval and pupal instars all contribute to its reduction. As the adult is the only instar capable of reproduction in most insects, the rate of oviposition of the whole population will depend upon the number of fertile females present and upon their average fecundity (rate of oviposition). Population growth will then be governed by the factors affecting natality, sex ratio and adult longevity, natality itself being determined by fecundity, the fertility of the eggs, and egg, larval and pupal mortality. If physical conditions remain constant and the organism itself does not change, all changes in these factors will be density-dependent. Crowding may then affect population growth through the limitation of (1) food or oxygen, or (2) space (leading to reflex stimulation caused by the presence of other individuals), or (3) the accumulation of metabolic waste and other products ('conditioning' of the medium). When precautions were taken to prevent the conditioning of the medium and to maintain the food supply at a constant level, competition for space, whether intraspecific or interspecific, played the most important role in determining the rate of population growth of these insects. This factor usually prevented the ratio of population to food supply reaching a value at which the latter would be insufficient. Oxygen lack was never observed. When the medium was allowed to become conditioned, such conditioning quickly rose to paramount importance and dominated population growth. The incidence of all these factors was upon natality, the sex ratio being never and adult longevity never importantly affected. Egg-fertility was also never affected.

In unconditioned wheat media, at densities possible in actual populations, reduction in fecundity of *Rhizopertha dominica*, *Sitotroga cerealella* and *Oryzaephilus surinamensis* was entirely due to competition for space for two purposes: oviposition and feeding in the two beetles, and for oviposition only in the moth (Crombie, 1942). Crowding thus affected fecundity through behaviour, and when two species were inhabiting the same environment their mutual effect upon each other's fecundity was greater in proportion to the similarity of their oviposition sites. It is crowding in relation to oviposition sites (e.g. the number of adults per wheat grain) and not crowding in relation to total space, which affects their fecundity. This seems to imply that the females of these species perceive their oviposition sites as such. The nature of this perception in *Rhizopertha dominica* has been analysed (Crombie, 1941). Scarcity of oviposition sites upsets the normal oviposition rhythm of

R. dominica and *Oryzaephilus surinamensis*, and leads the females to deposit their eggs in unusual places. While oögenesis in these two species is evidently adapted to a continuous although not complete restraint from oviposition while crowding is intense, in *Sitotroga cerealella* this is not so. An initial restraint is followed by a sudden burst of oviposition, due presumably to the pressure of egg production. But complete restraint may be exercised. The stimulus to oviposition in this species is tactile, depending on the presence of crevices. The females will die full of eggs rather than oviposit them in an empty glass dish which does not provide this stimulus. In unconditioned flour media reduction in fecundity of *Tribolium confusum* and *Oryzaephilus surinamensis* was also brought about by the competition for space, as was their mutual effect on each other when these two species inhabited the same medium (Crombie, 1943). In conditioned media the fecundity of all three beetles was reduced more or less in proportion to the degree, and irrespective of the species causing the conditioning. This effect seems to be due rather to 'poisoning' than to starvation, and is one of short duration upon oviposition rather than a lasting effect upon egg production (Crombie, 1942, 1943).

The behaviour of the ovipositing females is not well adapted to the care of the young. Although the rate of oviposition is reduced by crowding, it remains so high that a considerable mortality must occur in the immature stages before the offspring are reduced to numbers within the capacity of the environment to support them. The fate of the supernumerary young of *Tribolium confusum* and *Oryzaephilus surinamensis* is to be destroyed by adults and larvae (Crombie, 1943; Stanley, 1941, 1942, 1943). Eggs are destroyed in direct proportion to their density and the density of feeding stages present, and the same relationship may be supposed to hold for the destruction of pupae. In unconditioned media destruction of the young stages, particularly by the adults, is so much the most important factor reducing natality that the others may be ignored. This and the rate of oviposition alone determine the rate of population growth of each of these species, and the relative rates at which each destroys the young stages of the other also determines the result of competition between them. Here the less voracious and equally vulnerable *O. surinamensis* is at a considerable disadvantage. It does not attack the pupae of *Tribolium confusum* at all, and attacks its eggs at a lower rate than its own eggs are attacked by *T. confusum*. Any egg of the latter species which hatches is thus safe from *Oryzaephilus surinamensis*, while the latter, whose pupae are attacked by *Tribolium confusum*, is not safe from its rival until it emerges as an adult. In conditioned media larval and pupal mortality and the duration of the larval stage of *T. confusum* are, as Park (1938) and Park, Miller & Lutherman (1939) have shown, more or less proportional to the degree of conditioning, while eggs are unaffected.

At the highest densities reached in growing populations of *Rhizopertha dominica* and *Sitotroga cerealella* fecundity remained almost at its maximum (Crombie, 1944*a*). This means that the larvae must be adapted, particularly during the early instars, to an independent existence. They show an ability both to choose, by means of a chemical sense, objects composed of suitable food in which to develop and to avoid overcrowding by migrating from such objects (e.g. wheat grains) containing other larvae. The latter seems to be caused entirely by encounters within the wheat grain. There is no evidence that larvae perceive each other at a distance. Such encounters occur at random and result in fighting, followed by death or migration. This is entirely a competition for space. It occurs at densities far below that at which food would become scarce. With both species the average number of adults emerging per grain is 1·2 when larvae in any number greater than one enter a grain, whereas there is enough food present per grain to support approximately 4·5 *Rhizopertha dominica* and 3 *Sitotroga cerealella*. Among larvae of the same age neither conditioning of the medium nor lack of oxygen come into effect. It is probably for these reasons that larval crowding has no effect upon the size or fecundity of the adults into which they grow.

Except for a small unexplained 'intrinsic' mortality among the larvae of *Sitotroga cerealella*, larval mortality is entirely density-dependent and is the result of random encounters. With a limited number of wheat grains of course those migrating would merely die elsewhere. The probability that any particular larva will survive is then inversely proportional to the initial number i present, but the average number of larvae a which complete their development in one wheat grain remains constant at all values of i greater than l. Where P represents the proportion dying, the relationship between survival and density, expressed as the number of larvae per grain, is thus given by the equation $(1-P)=a/i$. This relationship, which when survival is plotted against density is hyperbola-like, holds for both species alone and in competition. In all cases $a=1{\cdot}2$. In interspecific competition between larvae, *Rhizopertha dominica* has a greater relative rate of survival than *Sitotroga cerealella* in the proportions $1{\cdot}3R:1S$. Mortality is greater the nearer the competing larvae are to the same age, the older usually standing at an advantage. With sufficient differences in age the number of larvae completing their development per grain rises above 1·2. In *S. cerealella* a certain proportion of larvae have atypical rates of development which thus enable them to survive competition for

space and take advantage of the available food supply where normal specimens would succumb. Since *S. cerealella* females lay large batches of eggs during a single bout of oviposition, e.g. upon one ear of wheat in the field, this feature of their biology probably increases their survival in nature. Mortality during the immature stages due to larval competition is thus by far the most important factor reducing natality in these two species, and with the rate of oviposition it may be considered to determine the rate of population growth of each species alone and in competition with the other.

This analysis of the factors determining the rate of population growth may now be used to explain the observed growth of populations of each species alone and in competition with others under controlled conditions (Crombie, 1945, 1946). Populations of each species alone began with a small number of individuals and competing species began with various initial numerical relationships. In flour, which is suitable for the development of *Tribolium confusum* and *Oryzaephilus surinamensis*, changes in the numbers of all instars could be observed by sieving the medium. This could not be done with *Rhizopertha dominica* and *Sitotroga cerealella* which require a different type of medium, e.g. wheat in the grain. In the latter only adults could be counted and changes in the immature instars were inferred from the detailed analysis already described.

Populations of each species living alone in media containing a limited food supply which was allowed to become conditioned, increased to maxima and then declined as the food became exhausted and waste products accumulated. As time passed the age composition of *Tribolium confusum* and *Oryzaephilus surinamensis* populations shifted from a majority of young stages to a majority of adults (Crombie, 1946). The decline of the populations was due mainly to the failure of the larvae to develop and pupate, but in *O. surinamensis* the cessation of oviposition also contributed to this effect. The size of *Sitotroga cerealella* adults decreased in succeeding generations and the longevity of *Rhizopertha dominica* was also reduced in conditioned media.

In media in which the amount of food was maintained at a constant level and conditioning was prevented, the adult populations of each of the four species rose to a maximum which was independent of the initial population and remained indefinitely fluctuating about this value. The adult populations of *Sitotroga cerealella* fluctuated violently because adults died before those of the next generation had emerged. The maxima were always below those which the food present could support and were therefore presumably determined by competition for space. A comparison of the rates of oviposition with the rates at which adults emerged showed that in the maximum populations there was an immense mortality in the immature stages. This amounted to over 90% with *S. cerealella* and over 99% with each of the other three species. The intensity of selection thus increased from a low value at the beginning of population growth to a very high value at the end.

Interspecific competition in unconditioned media was chiefly for space, whereas in media which began with a limited food supply which was not renewed it was chiefly for food, with conditioning as a contributory factor. As a result the competitive relationship between two species was sometimes different in the two kinds of medium, e.g. the competitive relationship between both *S. cerealella* and *Rhizopertha dominica*, and *Oryzaephilus surinamensis*, shifted slightly in favour of the former species in unrenewed as compared with renewed media. In a renewed medium this relationship probably depends chiefly on the destruction of eggs and pupae by adults and larvae, for which the more predaceous *O. surinamensis* is better placed. In an unrenewed medium the ability of the larvae to make the best use of the limited food supply is the determining factor, and here the other two species have the advantage. The competitive relationship between the latter remained the same in both media.

Species occupying different ecological niches survived together in the same medium while of those occupying the same niche one always exterminated the other. The results of competition in unconditioned media between different combinations of species are shown in Table 1. *Rhizopertha dominica* always eliminated *Sitotroga cerealella* from media of wheat because their larvae have similar needs and habits and those of the former species are intrinsically superior. *Rhizopertha dominica* thus excels *Sitotroga cerealella* in interference and it also does so in rate of reproduction and survival. Each generation of *S. cerealella* adults dies quickly, leaving its offspring as the sole representative of the species, whereas the gains made by each generation of *Rhizopertha dominica* larvae accumulate in the long-lived adults whose continuous oviposition gives succeeding generations of its larvae a tremendous majority, until *Sitotroga cerealella* decreases to zero. *Tribolium confusum* always eliminated *Oryzaephilus surinamensis* from media of flour where all individuals were equally open to attack. The former species excells the latter in interference (destruction of immature stages) and it also has a higher rate of reproduction and survival. But in crushed wheat and in flour containing pieces of glass tubing of a bore large enough for the larvae of *O. surinamensis* to enter and pupate in, but too small for the larvae of *Tribolium confusum*, the former species was able to survive side by side with the latter. With glass tubing of wider bore which *T. confusum* adults can enter, *Oryzaephilus surinamensis*

was exterminated as in plain flour. In wheat *Rhizopertha dominica* and *Sitotroga cerealella* survived together with *Oryzaephilus surinamensis*, and *Rhizopertha dominica* with *R. confusum*, because the larvae of the first two species develop and feed inside the grains and so avoid destruction by the adults and larvae of their competitors which feed in the open medium.

It is always convenient and may be instructive to express the results of a long series of observations in the form of a compact algebraic equation. If such an equation be merely empirical, it will be useful according as the accuracy with which it describes the observations themselves, and as the range over which it holds good increases. If it is to be more than empirical, then each of the parameters must represent a factor actually operating in nature (Gray, 1929). Here the function is assumed to be linear (Lotka, 1925, 1932; Volterra, 1926; Kostitzin, 1937; D'Ancona, 1942). In these experiments, these two species do to a first approximation inhibit each other's increase in this way, a single parameter in each equation representing the overwhelmingly important factor determining competition, the struggle between the larvae. The parameters of the logistic equation and the Lotka-Volterra simultaneous equations are thus to a first approximation related to each other in the same way as the biological processes which they represent, and these equations describe adult population growth with an accuracy commensurate with that of the observations. But because of the variability of the biological processes the experimental error is large. The biological assumptions of these equations are also not strictly true for *Tribolium confusum* and

Table 1. *Results of competition between species according to ecological niche (unconditioned media)*

	Sitotroga cerealella	*Oryzaephilus surinamensis*	*Tribolium confusum*
Rhizopertha dominica	*R.* exterminates *S.* in wheat: larvae similar, *R.* superior	Both survive in wheat: immature *R.* protected, *O.* not attacked	Both survive in wheat: immature *R.* protected, *T.* not attacked
Oryzaephilus surinamensis	Both survive in wheat: immature *S.* protected, *O.* not attacked		*T.* exterminates *O.* in flour: both eat immature stages but *T.* more voracious. Both survive in crushed wheat, or flour with tubing which protects *O.* pupae

Populations of *Sitotroga cerealella* are separated during growth into distinct generations, but population growth may be measured by considering only the sizes of successive generations of adults. With this adjustment, adult population growth of this species and of *Rhizopertha dominica* is determined by a statistically constant rate of oviposition and one overwhelmingly important density-dependent check, larval competition. Although, as shown above, the relationship between larval mortality and larval density is not linear, at the very high larval densities present this relationship does hold to a first approximation. At such densities, since the rate of oviposition may be considered unchanged, larval mortality is also approximately linearly related to adult population density. In the Verhulst-Pearl 'logistic' equation, population density is related to time by a constant representing the rate of reproduction and by a factor which reduces this in direct proportion to population density (Crombie, 1945). Two simultaneous logistic equations (the Lotka-Volterra equations) may be used to describe the growth of two species competing for the same limited environment, by the introduction of two other parameters ('competition coefficients') representing the notion that each species inhibits the increase of the other as a function of its own density. *Oryzaephilus surinamensis*. The rates of oviposition of these species are statistically constant; but since the checks to their increase depend on encounters between feeding (adult, larvae) and eaten (pupae, eggs) instars, these are related to population density not by a linear but by a quadratic factor (Crombie, 1946). But the divergence between the actual relationship between survival and density and the linear relationship assumed by the equations is no greater than the experimental error due to the variability of the rates of destruction of eggs and pupae. When 'competition coefficients', calculated from the observed relationships between density and the relative rates of destruction of the immature stages, were inserted into the Lotka-Volterra simultaneous equations, the latter were found to describe the growth of the competing populations in a rough way. Equilibrium positions which are independent of initial population densities were reached by populations of all the pairs of competing species studied. These equilibrium positions are described to varying degrees of accuracy by the Lotka-Volterra simultaneous equations (Figs. 1, 2 and 3).

In Park, Gregg & Lutherman's study (1941 of the competition between the beetles *Tribolium confusum*, *Gnathocerus cornutus* (Tenebrionidae) and *Trogo-*

derma versicolor (Dermestidae) in a medium of fine flour, coarse rolled oats and yeast, the outcome of competition often depended on the initial concentrations of the competing species (Park, 1943). Thus, when *Tribolium confusum* got well established it always drove out *Gnathocerus cornutus*, but when *Triboluim confusum* adult population was reduced to a low value, apparently by an epidemic protozoan densities of *Gnathocerus cornutus* this species always exterminated *Trogoderma versicolor*. *Gnathocerus cornutus* seems to inhibit (perhaps by predation) the pupation and emergence of the latter. When *Trogoderma versicolor* had the initially higher density, *Gnathocerus cornutus* was exterminated. The values of the constants of the Lotka-Volterra simultaneous equations roughly calculated for these two species

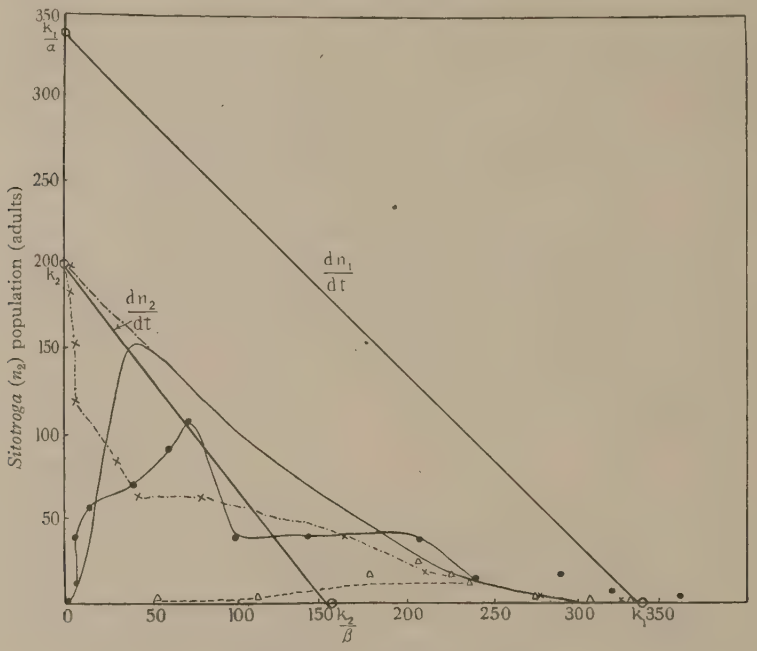

Fig. 1. Diagram illustrating the competition between *Rhizopertha* (n_1) and *Sitotroga* (n_2) in renewed wheat, with different initial concentrations. The theoretical curves were calculated from the Lotka-Volterra simultaneous equations. Two *Rhizopertha* versus 2 *Sitotroga*: •————• (observed), ———— (calculated); 50 *Rhizopertha* versus 2 *Sitotroga*: △ (observed), – – – – (calculated); 2 *Rhizopertha* versus 200 *Sitotroga*: ×–·–·–·–× (observed), –·–·–·– (calculated). The two broken theoretical curves eventually join the full theoretical curve. The *Sitotroga* were always exterminated.

$$dn_1/dt = k_1 - n_1 - \alpha n_2 = 0; \quad dn_2/dt = k_2 - n_2 - \beta n_1 = 0.$$

(Figure reproduced from Crombie (1945), *Proc. Roy. Soc.* B, 132: 362–95, Fig. 2, by permission.)

infection, this species was exterminated by superior numbers of *Gnathocerus cornutus*, which apparently eats its eggs, small larvae and pupae. If the *Tribolium confusum* adult population had not undergone violent oscillations it seems probable that it would always have exterminated *Gnathocerus cornutus*. *Tribolium confusum* always exterminated *Trogoderma versicolor*, irrespective of initial imaginal densities, at a rate roughly proportional to the initial concentration of the former species. With equal or superior initial

(see Crombie, 1946) usually correspond to the fourth condition of equilibrium (Crombie, 1945), where the inhibition of each species by the other is greater than its auto-inhibition, and it is initial densities which chiefly determine which species could survive together in the same environment. But the nature of the competition between them has not yet been fully analysed. When all three species competed (with equal initial numbers) the *Trogoderma versicolor* population fell steadily to zero after 90 days, and

Gnathocerus cornutus disappeared next after 510 days, leaving *Tribolium confusum* alone. (See p. 73.)

Two other examples of interspecific competition may be mentioned here. MacLagan (1932) found that competition between the moth *Sitotroga cerealella* and the grain weevil *Sitophilus granarius* (Curculionidae) reduced the rate of reproduction of each species. Vladimerova & Smirnov (1938, cited from Park, 1941) found that interaction between two species of house-fly stimulated the population growth of one while depressing that of the other.

(2) *Insect parasitoids.* Examples of interspecific competition are found among the larvae of insect parasites and parasitoids (Clausen, 1940) which commit multiparasitism in their hosts—the eggs, larvae or pupae of other insects. This, as Imms (1937) points out, usually occurs when the ovipositing females fail to distinguish parasitized from unparasitized hosts, and so depends upon an error of instinct. This occurs sometimes with the hymenopterous parasites of the moth *Plutella maculipennis* (Lloyd, 1940). In his review of this subject Imms (1937)

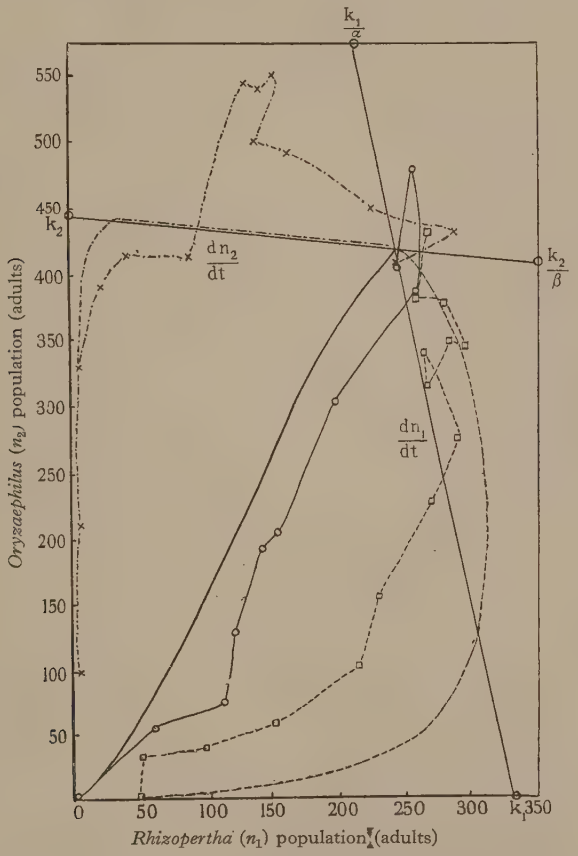

Fig. 2. Diagram illustrating the competition between *Rhizopertha* (n_1) and *Oryzaephilus* (n_2) in renewed wheat, with different initial concentrations. The theoretical curves were calculated from the Lotka-Volterra simultaneous equations. Two *Rhizopertha* versus 2 *Oryzaephilus*: ○————○ (observed), ———— (calculated); 50 *Rhizopertha* versus 2 *Oryzaephilus*: □----□ (observed), ---- (calculated); 2 *Rhizopertha* versus 100 *Oryzaephilus*: ×-·-· × (observed), —·—·—· (calculated). Both species survived together and their populations reached the same equilibrium point whatever the initial values (Crombie, 1945).

$$dn_1/dt = k_1 - n_1 - \alpha n_2 = 0; \quad dn_2/dt = k_2 - n_2 - \beta n_1 = 0.$$

(Figure reproduced from Crombie (1945), *Proc. Roy. Soc.* B, 132: 362–95, Fig. 7, by permission.)

distinguishes three categories: where only one species of parasite survives, where both survive and where none survives. Those in the last category usually die through lack of food. The winner in the first category is frequently the one which first attacks the host and so reaches the destructive feeding stage before its rivals. Parasite larvae frequently attack one another within the host, while others kill rivals by toxic secretions. The competitive relationship between species in the second category calls for special investigation: little is known about them.

During competition between the solitary hymenopterous parasites *Pteromalus puparum* and the gregarious *Hemiteles melanarius* (Martelli, 1907) or *Pimpla instigator* (Picard, 1922), the latter were always exterminated. *P. instigator* was also destroyed by the tachinid fly *Compsilura* which eats the organs of the host (the cabbage white butterfly (*Pieris brassicae*)) before pupating. Parker (1933) found that when the hymenopterous parasites *Anastatus disparis* and *Oenocyrtus kuvanae* both attacked the same egg of their host (the gipsy moth, *Porthetria dispar*) either both

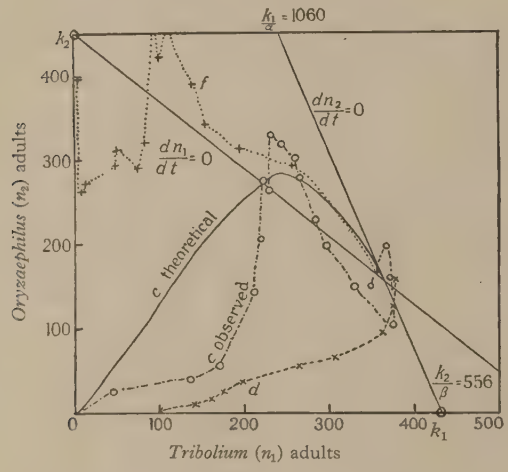

Fig. 3 (*a*)

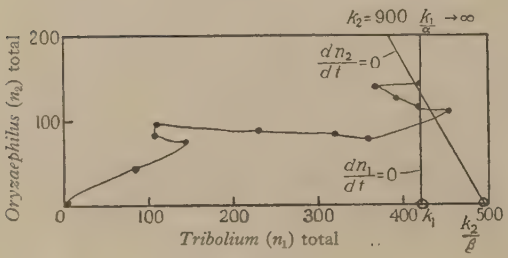

Fig. 3 (*b*)

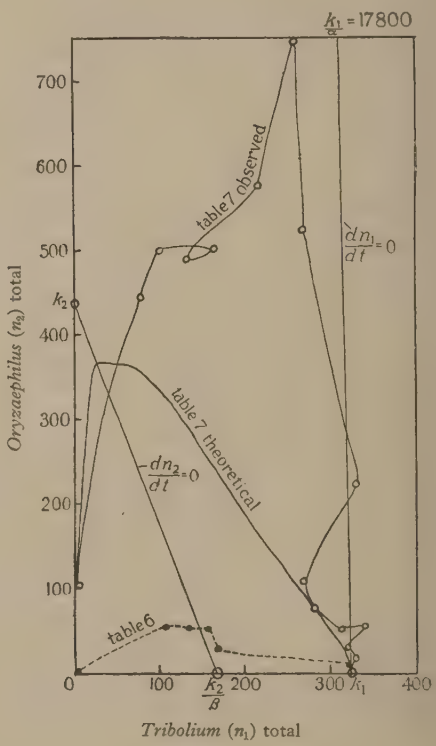

Fig. 3 (*c*)

Fig. 3. Diagrams illustrating the competition between *Tribolium* (n_1) and *Oryzaephilus* (n_2) in various renewed media, with different initial concentrations. (*a*) *Wheat*: the curves represent respectively changes in adult populations which began with the following initial values: 4 *Tribolium* versus 4 *Oryzaephilus* (curve *c*); 100 *Tribolium* versus 4 *Oryzaephilus* (curve *d*); 4 *Tribolium* versus 400 *Oryzaephilus* (curve *f*). (*b*) *Fine flour with 1 mm. bore glass tubing*: the curve represents changes in total populations (eggs, larvae, pupae and adults) beginning with 4 adults of each species. (*c*) *Fine flour*: the curve represent respectively changes in total populations which began with the following initial values: four adults of each species (Table 6); 4 *Tribolium* and 100 *Oryzaephilus* adults (Table 7). The theoretical curves were calculated from the Lotka-Volterra simultaneous equations. In (*a*) and (*b*) both species survived together and their populations reached the same equilibrium point whatever the initial values. In (*c*) the *Oryzaephilus* were always exterminated (Crombie, 1946).

$$dn_1/dt = k_1 - n_1 - \alpha n_2 = 0; \quad dn_2/dt = k_2 - n_2 - \beta n_1 = 0.$$

(Fig. reproduced from Crombie (1946), *Proc. Roy. Soc.* B, 133: 76–109, Fig. 10, by permission.)

parasites died before reaching maturity or *Anastatus disparis* survived alone if it attacked the host while its rival was in an early larval instar. But in the field there would be no serious competition between the total populations of the two species unless the parasitism approaches the limit of the available host eggs. According to Smith (1933) the larvae of the hymenopteran *Scutellista cyanea* preys on the eggs of the black scale *Saisseta oleae*, which are found beneath their parent's body. When the former insect was introduced from South Africa into California the native hymenopteran *Tomocera californica*, which has almost identical habits with *Scutellista cyanea*—its larvae also feeding on the eggs of *Saisseta oleae* beneath the parent scale (Clausen, 1940, p. 210), was almost although not entirely eliminated.

(3) *Field observations.* Lloyd, Graham & Reynoldson (1940) and Lloyd (1943*a*, *b*) studied, by continuous trapping for several years, the competition occurring between several species of dipterous larvae and a worm in sewage beds. The fauna of these bacteria beds is a balanced one and comprises in particular the oligochaete worm *Lumbricillus lineatus* (Enchytraeidae), the flies *Psychoda* spp. (Psychodidae), *Metriocnemus* spp. and *Spaniotoma minima* (Chironomidae). The seasonal abundance of the different species depends chiefly on the weather which influences *Metriocnemus longitarsus* and *Lumbricillus lineatus*, the dominant forms in the upper region of the bed, and these affect the other species by competition. Weather also directly affects the subordinate forms. There are three lines of evidence for competition. First, the expected monthly abundance was calculated from the speed of life cycle at different temperatures and compared with the actual abundance. In spring and early summer the *Psychoda* are most abundant, but from about May their numbers fall below the expected figures. This coincides with the abundance of *Metriocnemus*, *M. longitarsus* larvae forming a barrage in the upper layers, followed by the midsummer maximum of *Spaniotoma minima* when *Metriocnemus longitarsus* declines because of its habit of feeding and pupating near the surface where it suffers from drying. *M. hirticollis* has a major flight slightly later than *M. longitarsus*, and so is also dependent for its summer establishment on the number of the latter. In autumn *M. longitarsus* again increases, causing a decline in *Spaniotoma minima* below its expected numbers and preventing any increase in the *Psychoda*. Secondly, in a neighbouring sewage works from which the *Metriocnemus* were absent and where (probably because of the lack of competition from them) *Spaniotoma minima* reached its maximum later, the summer depression of the *Psychoda* was much less pronounced. Thirdly, differences in the relative abundance of the flies in different parts of the beds are determined to some extent by the sweeping action of the sewage distributor. The *Psychoda* larvae tend to occur most abundantly in parts not favoured by the chironomids, although in the absence of the latter their distribution would be more uniform. Also, although the *Psychoda* larvae prefer the upper layers of sewage in the neighbouring works where the *Metriocnemus* are absent, in the presence of these organisms (which also prefer the upper layers) the *Psychoda* are found in greatest density below this zone. Where the larvae of *Spaniotoma minima* are reduced in the depths by the abundance of *Metriocnemus longitarsus* larvae the psychodids, which probably always oviposit to some extent there, are able to extend their period of abundance later in the year. The chief element in competition seems to be the predatory tendency of the chironomid larvae. This is in keeping with the structure of the mouth parts. Most of the destruction occurs to the eggs. Besides such direct attacks the larvae and the worms affect each other during grazing by loosening eggs, pupae and worm cocoons from the medium. Over-population may occur locally at some seasons of the year. Evidence of competition for food is found in the increased mortality of *M. longitarsus* and a reduction in weight of the emerging flies of this species and of *Spaniotoma minima*. *Lumbricillus lineatus* enters chiefly as a competitor for food, particularly after warm winters when it breeds more rapidly and causes an earlier spring deprivation for the larvae of *Metriocnemus longitarsus* and *Psychoda severini*.

Ecological succession of insect species in carcasses has been observed by Holdaway (1930) and Fuller (1934). These authors believe that the succession of dominant species is determined by two factors, first, the changes going on in the carcass itself, each stage of decomposition being characterized by a particular group of insects, and secondly, by competition. With the flies competition occurs chiefly among the larvae and often limits the niche they occupy (Evans, 1936). Interspecific interference apparently reduces the generation size of tsetse flies, *Glossina* spp. (Jackson, 1945). In a review of insect outbreaks in Europe Carpenter (1940) states that fluctuations in population are a general phenomenon of a large area. While fluctuations in the population as a whole cannot be characterized by any individual species, in years when a larger insect population occurs there is great upsetting of the biotic balance. This is shown by the decrease or increase in numbers of species which have characteristically prolonged periods of outbreak. Very often concurrently outbreaking species fall into the same ecological niche. Then in subsequent outbreaks in the same area the same species may not always take the lead, but one of the former subordinate species may reach the greatest abundance.

(4) Drosophila *mutants*. Finally, attention may be drawn to competition between different species or genotypes of *Drosophila*. Morgan & Tice (1914) observed that the expected hereditary ratios in *Drosophila* populations were changed by overcrowding, probably by differential mortality in the immature stages (Hammond, 1939). Timoféeff-Ressovsky (1933, 1935) studied experimentally the competition in artificial media between *D. melanogaster* and *D. funebris* and between races of the latter from different geographical regions. In mixed cultures of larvae the relatively more successful was the species or race the temperature of whose natural habitat corresponded most closely to that at which the experiments were conducted (Timoféeff-Ressovsky, 1940). Gagarin (1933, cited from Bodenheimer, 1938, p. 147) found that in mixed populations of *Drosophila* nearly all the mutants are eliminated by the wild type after a few generations. L'Héritier (1937) reviews the physiological differences between different allied species, especially of *Drosophila*, and describes experiments designed to study the hereditary basis of such differences. Different hereditary lines of wild type *D. melanogaster* were put in competition with various mutants from which they are distinguishable morphologically. Food was exposed to the simultaneous oviposition of the two competitors and competition occurred among the larvae. When oviposition was not simultaneous the eggs laid first had the greater chance of becoming adults. The relative success of the different lines was the same when competing with any of the mutants and corresponded to the order of resistance of the adults to starvation. L'Héritier & Teissier (1935) studied the competition between *D. melanogaster* and *D. funebris* in artificial media with a constant food supply and found that, whatever their initial concentrations, equilibrium was established with a large population of the former and a small one of the latter species. But the precise part of the food for which competition occurred is not known (Robertson & Sang, 1944*a*, *b*). Cheruwimov (1932) and L'Héritier & Teissier (1937) studied under experimental conditions, and Olenov *et al.* (1937) and Gordon (1939) by releasing mutants among natural populations, the rate of elimination of certain forms. Their results do not fully agree, some finding that the mutants disappeared altogether and some that they maintained themselves in a balanced population with the wild type. The conditions of competition here need further investigation.

(*f*) *Vertebrates*

A number of examples are described in §3 where differences in structure, habits or distribution between congeneric species of vertebrates may, according to the argument developed in §1, be attributed to competition, or where competition may be inferred from the fact that the animals eat the same food. There seem to be comparatively few direct observations of interspecific competition in this group. Gause (1934) quotes an example of competition among fish described by Kashkarov. When the wild carp, *Cyprinus albus*, was introduced into lakes inhabited by *Schizothorax intermedius*, the latter was gradually eliminated because the carp eats its spawn. The competition of introduced species for the same resources seems to have been at least partly responsible for the disappearance of native species of fish, birds and mammals in New Zealand, although it is difficult to separate this from the undoubted effect of introduced predators and the disturbance of habitats by man (Thompson, 1922). Formosof (1933) claimed that decreases in squirrel numbers in Siberia correspond to invasions of the Siberian nutcracker, *Nucifraga caryocatactes macrorhynchus*, which competes for the same food. In Britain at the present time the native red squirrel, *Sciurus vulgaris*, appears to be decreasing rapidly before the introduced grey squirrel, *S. carolinensis*. The black rat, *Rattus rattus*, seems to have suffered in the same way from the competition of the brown rat, *R. norvegicus*, in temperate Europe. The former is considered to have been imported into Europe from Asia at the time of the Crusades and became a serious pest during the Middle Ages. The brown rat, also from the East, invaded Europe in the eighteenth century and, corresponding to its increase, the black rat has practically disappeared from temperate latitudes to which it is less well adapted than its rival, while in warm climates and in environments where its superior climbing ability is an advantage (e.g. in buildings) it apparently holds its own (Barrett-Hamilton & Hinton, 1910–21; Hinton, 1918).

3. DIFFERENCES IN DISTRIBUTION, STRUCTURE AND HABITS ATTRIBUTABLE TO COMPETITION

In many of the examples given of competition between species with similar ecology, neither the factors controlling population density nor the ecological relations between the competitors are accurately known. But where these details have been investigated, it proves that, in keeping with the theoretical demonstration set out in §1*c*, species with the same needs and habits cannot survive together in the same place when the ratio of population density to environmental resources reaches a value at which competition occurs. Such species are not necessarily taxonomically related. This principle, as Darwin has pointed out, is likely to have two kinds of effects on organisms in nature: (1) on their dis-

tribution and abundance, and (2) on their evolution. Two important points raised by this survey need special emphasis. The first is the necessity of making often the most detailed study of the needs and habits of an organism. Often the very slightest differences, birds feeding at slightly different levels of the vegetation or at slightly different times or small differences in food preferences, may enable species in other respects very similar to survive together (Vestal, 1914). The second point is that adaptive differences between related species (or races) are often not in evidence until competition between them has been observed (Lack, 1944).

(*a*) *The effect of interspecific competition on distribution and abundance*

The importance of interspecific competition in ecological succession has already been mentioned, and Beauchamp & Ullyott (1932) have shown how it may affect the distribution of organisms in nature. Elton's (1944, 1946) study of 'fifty sample surveys in widely different habitats and parts of the world' suggests that it may determine the structure of animal communities.* He found 'a rather constant relationship between the number of species and the number of genera present. This relationship suggests that species belonging to the same genus tend strongly not to occur in the same area of any major habitat at the same time; that this is attributable to competition for resources available in a particular ecological niche; that apart from this, the main extra-specific ecological relations between animals in a community are those between genera; that the genera chosen by the majority of taxonomists are ecological realities; and that, as previously indicated by the limited numbers of species in an animal community, the latter is an organization with strictly limited membership determined by very definite laws. From this hypothesis it would follow that the successful introduction of a new species will usually cause the decrease, often disappearance, of one of the species already present. The empirical relationship established here for the relation of species to genera seems to apply also to plant associations' (Elton 1944; see also de Candolle, 1820 and Darwin, 1859, p. 115). An analogous explanation may help to account for the definite relationship often found between the number of species and the number of individuals in a random sample of an animal population. Garthside (cited by Chapman, 1931, p. 398, and Graham, 1933) and Fisher, Corbet & Williams (1943) found that while a few, often only one, insect species are characterized by a large number of individuals, most occur in relatively small numbers. Lloyd, Graham & Reynoldson (1940) and Reynoldson (1942) observed the same phenomenon in bacteria sewage beds, where one species dominated the insect fauna and the fungus flora respectively. Gause (1936) refers to the same relationship among plants (cf. Jaccard 1912, 1941) and other organisms. Such a definite relationship between the numbers of different species in a given environment could be brought about either by some regularly acting environmental factor or by interaction between the species themselves. Interaction could bring about such a relationship in two ways. The numerous rare species may create a favourable environment for the few numerous species, or the latter may behave as dominants and by competition eliminate the rare species from all but a few ecological niches in which they can hold their own. Whether either of these explanations is correct or not, the subject would repay investigation.

(*b*) *Interspecific competition and evolution*

Reproductive isolation between different members of a species, leading to the formation of new species, seems to be initiated in at least two different ways: by genetic changes and by some form of geographical or ecological isolation. The evolutionary role of competition between the divergent forms varies according to whether they interbreed or not.

(1) *Reproductive isolation initiated by genetic factors.* Mayr (1942) uses the term 'instantaneous sympatric speciation' to designate 'the production of a single individual (or the offspring of a single mating) which is reproductively isolated from the species to which the parent stock belongs. Such an individual would be the potential ancestor of a new species.' Several processes are known among plants, e.g. polyploidy of different kinds (Darlington, 1937, Dobzhansky, 1941), which would produce this result. Polyploidy is rare among animals since it interferes with the sex-chromosome mechanism (Dobzhansky, 1941), but Hogben (1940) has listed a number of methods by which instantaneous sympatric speciation could occur. These are: '(i) hermaphroditism combined with the possibility of self-fertilization, (ii) the existence of a separate spore-forming generation, (iii) parthenogenesis, (iv) production of individuals of either sex by clones from the same soma, (v) polyembryony, (vi) obligatory close-inbreeding, (vii) the occurrence of an epidemic of similar mutations at the same time. Restriction of the reproductive season and intense assortative mating in one form or another may also establish a partial species-barrier and enable species-differentiation to proceed by selection in the same environment from a different genetic basis. Such a barrier may gradually become a complete obstacle to interbreeding in the environment, and all stages

* [See, however, the paper by C. B. Williams (1947) in this *Journal*, 16: 11–18. Editor.]

of this process can be illustrated in moths' (see Darlington, 1940; Wright, 1940; Huxley, 1942; Mayr, 1942). Unless differences in needs and habits arise at the same time, it seems likely that, with the establishment of such breeding barriers, competition between the divergent forms will lead to the extinction of one of them. This seems to have happened among the Protozoa with different mating types already mentioned (Gause, 1942, see §2(*c*)). Another example is the inter-tidal grass *Spartina townsendii*, an allotetraploid of the European *S. stricta* crossed with the American *S. alternata* (Huskins, 1931). *S. townsendii* is apparently superior to both parents, not only eliminating them in competition but extending its range beyond theirs (cf. Clausen, Keck & Hiesey, 1940, pp. 422–3). Similar examples are given by Huxley (1942, pp. 328 et seq., 386).

(2) *Reproductive isolation initiated by spatial isolation.* It seems likely that genetic divergence between two populations consisting of members of the same species is usually preceded by some form of geographical or ecological isolation (Robson & Richards, 1936; Dobzansky, 1941; Huxley, 1940, 1942). Here, where at least at first genetically controlled breeding barriers are absent, a mutation is potentially able to enter into the genetic constitution of the whole species, and is only prevented from doing so by the mode of isolation in operation. Different authors place different emphasis on the roles of geographical and ecological factors in isolation. Lack (1940, 1944, 1945, 1947) believes that with birds new species have arisen primarily through geographical isolation, and that ecological isolation is enforced through competition when two species later meet in the same area. He argues against genetic divergence among birds arising out of ecological differences alone, that the latter do not provide sufficient barriers to interbreeding. Mayr (1942) extends this objection to other organisms, remarking that in the absense of sexual isolation most forms of non-geographical divergence would be swamped by crossing between divergent forms (cf. Dobzhansky, 1941). But as Thorpe (1945) has recently pointed out, it is probably better to regard geographical, topographical and ecological isolation as different degrees of spatial isolation. Furthermore, this theoretical difficulty seems to have been overcome by the work of Mather (1943), who has shown that breeding barriers (isolation mechanisms) are likely to arise between any two populations where any factor—genetic, geographical, ecological or anything else—causes them to breed less freely with each other than each does within itself. After isolation mechanisms have arisen other differences between the two populations will accumulate, selection within each group tending to make each better adapted to its own habitat (in the sense of the parts of the physical and biological environment which affect it) than to that of the other. Members of each group would thus be at a disadvantage in the habitat of the other and competition between them with its consequent mortality will be greater the closer their needs and habits. There will therefore be selection both for differences in needs so that each makes different demands from the environment and for differences in habit, e.g. differences in behaviour, which tend to confine each to its own ecological niche. Such selection will continue until the two groups have diverged so far that competition no longer occurs.

After a careful study, Robson & Richards (1936) came to the view that it could not be concluded from the evidence available that differences in habit and structure between animal species are usually adaptive, adaptive differences appearing only between the higher taxonomic categories. The argument developed above makes it seem likely, however, that specific differences will be found to be usually adaptive. Lack (1944, 1945, 1947) has shown this to be true of many birds. As Lack (1944) points out, the presence of adaptive differences between closely related species of plants from different habitats is frequently very difficult to determine until one is transplanted into the natural habitat of the other, when it is usually quickly eliminated (cf. Sukatschew, 1928; Timoféef-Ressovsky, 1933, 1935). Circumstances under which random non-adaptive changes may accumulate in small populations have been described by Wright (1940). Another such circumstance would be if some factor such as predators or parasites kept a population of organisms in otherwise favourable circumstances more or less permanently below the density at which competition for environmental resources occurs, when the only form of selection would be for resistance to this factor. The survival of different variants would then be unrelated to their adaptive value in other respects and many of the differences between species originating thus may be unadaptive.

Whatever the cause of their divergence, related species which occur in the same area will tend to compete if the ratio of population to resources is high enough. It would then be expected that either one will completely eliminate the other from that area, resulting in geographical separation, or that they will survive together with some form of ecological isolation. The conclusion of Darwin's argument would thus be fulfilled. In fact, in all cases where such species have been studied, this conclusion proves correct.

Lack (1944, 1947) has made a survey of the ecological relations between congeneric species of birds on remote islands, in the finches of the Galapagos and in the passerine birds breeding in Britain. Related forms in the same area are thought to have met again after differentiation in isolation. In the

groups studied all related species, except for a few which need further investigation, reach one or other of the following stable positions. Either one species eliminates the other, or the two species occupy separate geographical regions or different habitats in the same region, or they live together in the same habitat and region but eat mainly different foods. The last is often achieved where the two species differ markedly in size. The type of ecological isolation found between two species may change seasonally or regionally. Lack (1945) studied the ecological relations between two related species of British non-passerine birds, the cormorant and the shag, which overlap in geographical range, and found that they differ markedly both in nesting sites and food. The same rule applies to German hawks and owls: no two congeneric species compete for food in the same habitat (Lack, 1946). Further, when species in different genera are compared, no two compete for the same food supply, with the apparent exception of the predators of the vole, *Microtus arvalis*. The latter forms the staple food of several species of hawks and owls, of which up to five (none congeneric) may occur together in the same habitat. The suggestion, which needs investigation, is made that these predators do not effectively compete with each other because for most of the time *Microtus* is superabundant, while when there is a vole minimum, each predator perhaps turns to a different prey. Gause (1934) quotes an observation by Formosov on four species of terns (*Sterna*) which nest together but differ in feeding habits. One feeds on land on insects, and the other three on fish, but they differ in size and the distance from shore at which they hunt. There are also examples among mammals, of which Lack (1944, 1945) quotes several, of differences in habitat and distribution which may be attributed to competition between related species, e.g. between the common hare *Lepus europaeus* and *L. timidus* and between the two European bank voles *Clethrionomys* (=*Evotomys*) *glareolus* and *C. nageri* (Barrett-Hamilton & Hinton, 1910–21). Similar examples of differences between congeneric species are cited by Huxley (1942, pp. 280 et seq.). Wilson (1907) observed that four species of Antarctic seals belonging to different genera live in the same habitat but on different food (see Bertram, 1940). Among amphibians, Noble & Evans (1932) remark that the selection of different habitats, due to different climbing abilities and avoiding reactions, enables the salamanders *Desmognathus f. fuscus* and *D. f. carolinensis* to avoid competition and inhabit the same area.

In his study of the gall wasp genus *Cynips*, which forms galls on oaks, Kinsey (1930), after examining 17,000 insects and 54,000 galls, came to the conclusion that (with one possible exception) in each geographical area there is but one species (of the 93 into which he divides the genus) on any given species of host. The same rule applies to the 63 species of the gall wasp *Neuroterus* (Kinsey, 1923). In apparent contradiction with Kinsey (1930), Hogben (1940) remarks that 54 species of the family Cynipidae infest a single plant species (the oak). Several species of gall, sometimes of the same genus, 'are commonly found together on the same tree and the same leaf of the same tree'. But as no details are given it is impossible to tell whether the species in question make the same demands on the host and whether their populations reach sufficiently high densities for competition to occur.

Many examples of related species which differ either in distribution or ecology are given by Robson (1928), Thorpe (1930, 1940), Robson & Richards (1936), Diver (1940), Dobzhansky (1941), Huxley (1942), and Mayr (1942). Others seem to differ in neither fashion. These and other related species of organism living in the same area should be subjected to ecological analysis of the kind Lack (1944, 1945, 1946, 1947) has made with birds. Insects, about whose feeding and other habits a great deal of information has already been collected, would provide particularly suitable material for such a study. For instance, larvae of related species of Lepidoptera (Brues, 1920, 1936; Meyrick, 1928) and leaf miners (Hering, 1926; Needham, Frost & Tothill, 1928) are frequently restricted to different (but often related) species or genera of plants. Related species of parasitic insects from the same region also often attack different although related groups of hosts. This occurs in the ichneumonids studied by Mell & Heinrich (1931) and other examples are to be found in the 'Parasite Catalogue' (Thompson 1943–45). In Great Britain, among bees of the genus *Psithyrus*, which infest the nests of bumble-bees, each species is apparently associated with different species of host (Sladen, 1912). The ecological relationships between related species of freshwater mussels (Unionidae) whose glochidia attack fish (Howard & Anson, 1922), and between related species of parasitic Crustacea (Caullery, 1922) and other forms (Pearse, 1939, p. 526) would also well repay careful study. In such an investigation it would be necessary to take every species (and race) in the whole group and to analyse at every stage of the life-cycle both their differences and similarities in ecology (structure, habits) and distribution, and all the factors controlling their population density—physical, intraspecific and interspecific. Investigations of this sort would provide a more accurate knowledge of the nature of the differences between related organisms—e.g. how far they are adaptive—and of the ecological factors involved in the origin of species: a kind of knowledge which Darwin himself sought.

4. SUMMARY

1. Darwin argued from the observation that the potential rate of increase of organisms is greater than that which the resources of the environment can support, that many must perish from the action of the physical environment and of predators, parasites, etc. and from competition. When competition occurs it is severest between organisms with similar needs and habits, and since related organisms, particularly those which have just diverged from the same parent stock, will be most similar in this respect, competition will be severest between them until its own influence causes further divergence. Hence as new forms appear in a given locality, whether by evolving there or by migration after divergence elsewhere, they will either eliminate or be eliminated by their nearest relations unless each diverges so far from the other that competition between them ceases. Then all may survive together, each adapted to its own special habitat. This thesis has been considered by examining examples of competition between different varieties and species under experimental and natural conditions, and the ecology and distribution of related varieties and species in nature.

2. Three kinds of factors are involved in preventing the unlimited increase of an organism: the organism itself (i.e. its adaptation to the environment), the physical environment and the biological environment. The operation of biological environmental factors is usually density-dependent, while that of physical environmental factors is usually independent of population-density. Except for the very improbable event of a density-independent factor allowing an organism exactly to replace its numbers from generation to generation, only density-dependent factors can permanently control population density.

3. Competition may be defined as the demand at the same time by more than one organism for the same resources of the environment in excess of immediate supply. Only density-dependent factors are directly involved in competition, although density-independent (e.g. physical) factors may, through the competing organisms' own adaptations to environmental conditions, determine its results and also whether it occurs at all.

4. Competition occurs between organisms with similar needs and habits when the ratio of their population to environmental resources reaches a certain value. This ratio may be kept low and competition reduced or prevented by various agencies, e.g. climatic or other physical rigours, predators, parasites, other competitors, a rapid increase in environmental resources, regulation of their rate of reproduction by the organisms themselves, or changes in their nature.

5. If external conditions (other than those brought about by the organisms themselves, for these are part of the process of competition) remain constant enough not to reverse the competitive relationship between them, it can be demonstrated by a simple argument, of which the conclusion seems inescapable, that if two species have *identical* needs and habits they cannot survive together in the same place if they compete for limited resources unless they are exactly balanced in competitive advantage. The same conclusion applies to organisms with *similar* rather than identical ecology, but the necessary degree of similarity can only be discovered empirically. One species may be superior to another either in the combined rate of reproduction and survival independent of interspecific interference, in interference or in numbers. The chance of their being equally balanced is almost infinitely small.

6. Reference is made to work on the population growth of organisms of many kinds from bacteria to man, and competition between different species and varieties is analysed in examples from bacteria, fungi, yeasts, higher plants, Protozoa, planarians, crustaceans, freshwater lamellibranchs, phytophagous and entomophagous insects, mutants of *Drosophila*, fish, amphibians, birds and mammals. In many of the examples neither the factors controlling population density nor the ecological relations between competing species are accurately known; but where these have been investigated the theoretical conclusion described in the previous paragraph proves correct.

7. This principle, that competing organisms with the same needs and habits cannot survive together in the same place, can be used to explain the distribution and abundance of many species in nature and the structure of natural communities (e.g. the relation between the numbers of species and genera). It must also affect speciation. When genetic factors (e.g. polyploidy) initiate breeding barriers and divergence, unless differences in needs and habits arise at the same time, competition between the divergent forms will lead to the elimination of one of them. This seems to have happened in the grass *Spartina*. It seems likely, however, that genetic divergence between two populations consisting of members of the same species is usually preceded by some form of geographical or ecological isolation. Different authors place different emphasis on the roles of these two factors.

8. But whatever the cause of their divergence, related species which occur in the same area will tend to compete if the ratio of population to resources is high enough. It would then be expected that either one will completely eliminate the other from that area or that they will survive together by evolving some form of ecological isolation. In all cases where such species have been studied this proves to be so,

thus fulfilling the conclusion of Darwin's argument. This argument suggests that differences between species and races are usually adaptive, although in special circumstances they may not be.

9. There is need for extensive ecological studies, such as that carried out by Lack on birds, of the ecology and distribution of whole groups of related species. Investigations of this sort would provide a more accurate knowledge of the nature of the differences between related organisms, and of the ecological factors involved in the origin of species.

REFERENCES

Allee, W. C. (1927). 'Animal aggregations.' Quart. Rev. Biol. 2: 367–98.

Allee, W. C. (1931). 'Animal aggregations. A study in general sociology.' Chicago.

Allee, W. C. (1934). 'Recent studies in mass physiology.' Biol. Rev. 9: 1–48.

Allee, W. C. (1941). 'Integration of problems concerning protozoan populations with those of general biology.' Amer. Nat. 75: 473–87.

Andrewartha, H. G. (1944). 'The distribution of plagues of *Austroicetes cruciata* Sauss. (Acrididae) in Australia in relation to climate, vegetation and soil.' Trans. Roy. Soc. S. Aust. 68: 315–25.

Aubréville, A. (1938). 'La forêt coloniale (Les forêts de l'Afrique occidentale française).' Ann. Acad. Sci. Colon., Paris, 9: 1–244.

de Bach, P. & Smith, H. S. (1941*a*). 'The effect of host density on the rate of reproduction of entomophagous parasites.' J. Econ. Ent. 34: 741–5.

de Bach, P. & Smith, H. S. (1941*b*). 'Are population oscillations inherent in the host-parasite relation?' Ecology, 22: 363–9.

Banta, A. M. (1937). 'Population density as related to sex and to evolution in Cladocera.' Amer. Nat. 71: 34–49.

Beauchamp, R. S. A. (1932). 'Some ecological factors and their influence on competition between stream- and lake-living triclads.' J. Anim. Ecol. 1: 175–90.

Beauchamp, R. S. A. & Ullyott, P. (1932). 'Competitive relationships between certain species of freshwater triclads.' J. Ecol. 20: 200–8.

Berg, K. (1934). 'Cyclic reproduction, sex determination and depression in the Cladocera.' Biol. Rev. 9: 139–74.

Bertram, G. C. L. (1940). 'The biology of the Weddell and crabeater seals: with a study of the comparative behaviour of the Pinnipedia.' British Graham Land Expedition 1934–37, Sci. Rep. 1, No. 1: 1–139.

Bodenheimer, F. S. (1937*a*). 'Population problems of social insects.' Biol. Rev. 12: 393–430.

Bodenheimer, F. S. (1937*b*). 'Studies in animal populations. II. Seasonal population-trends of the honeybee.' Quart. Rev. Biol. 12: 406–25.

Bodenheimer, F. S. (1938). 'Problems of animal ecology.' Oxford.

Bonar, J. (1931). 'Theories of population from Raleigh to Arthur Young.' London.

Braun-Blanquet, J. (1932). 'Plant sociology. The study of plant communities.' Translated, revised and edited by G. D. Fuller and H. S. Conard. New York.

Brues, C. T. (1920). 'The selection of food-plants by insects, with special reference to lepidopterous larvae.' Amer. Nat. 54: 313–32.

Brues, C. T. (1923). 'Choice of food and numerical abundance among insects.' J. Econ. Ent. 16: 46–51.

Brues, C. T. (1936). 'Aberrent feeding behavior among insects and its bearing on the development of specialized food habits.' Quart. Rev. Biol. 11: 305–19.

Buchanan, R. E. & Fulmer, E. I. (1928–30). 'Physiology and biochemistry of bacteria.' Vols. 1–3. London.

Burkenroad, M. D. (1946). 'Fluctuations in abundance of marine animals.' Science, 103: 684–6.

Bystrikov, F. U. (1931). 'The root system of cultivated plant-competitors.' Bull. Appl. Bot., Leningr. 27, No. 5: 71–111. (In Russian with English summary.)

Cahn, A. R. (1929). 'The effect of carp on a small lake: the carp as a dominant.' Ecology, 10: 271–4.

Cain, S. A. (1939). 'The climax and its complexities.' Amer. Midl. Nat. 21: 146–81.

de Candolle, A. P. (1820). 'Dictionnaire des sciences naturelles.' Ed. F. G. Levrault. Strasbourg. Vol. 18 (GA–GJU): 359, 'Géographie botanique'.

Carpenter, J. R. (1939). 'The biome.' Amer. Midl. Nat. 71–21: 75–89.

Carpenter, J. R. (1940). 'Insect outbreaks in Europe.' J. Anim. Ecol. 9: 108–47.

Caullery, M. (1922). 'Le parasitisme et la symbiose.' Paris.

Chapman, R. N. (1931). 'Animal ecology with especial reference to insects.' New York, etc.

Chapman, R. N. (1939). 'Insect population problems in relation to insect outbreak.' Ecol. Monogr. 9: 261–9.

Cheruwimov, J. S. (1932). 'Analyse des Verhaltens eines geschlechtsgebundenen Merkmals in der Population.' Z. Indukt. Abstamm.- u. VererbLehre 62: 204–12.

Clausen, C. P. (1940). 'Entomophagous insects.' New York, etc.

Clausen, J., Keck, D. D. & Hiesey, W. M. (1940). 'Experimental studies on the nature of species. I. Effect of varied environments on western North American plants.' Publ. Carneg. Instn. No. 520: 1–452.

Clements, F. E. (1916). 'Plant succession: an analysis of the development of vegetation.' Publ. Carneg. Instn. 242: 1–512.

Clements, F. E. & Shelford, V. E. (1939). 'Bio-ecology.' New York, etc.

Clements, F. E., Weaver, J. E. & Hanson, H. C. (1929). 'Plant competition: an analysis of community functions.' Publ. Carneg. Instn. No. 398: 1–340.

Crombie, A. C. (1941). 'On oviposition, olfactory conditioning and host selection in *Rhizopertha dominica* Fab. (Insecta, Coleoptera).' J. Exp. Biol. 18: 62–79.

Crombie, A. C. (1942). 'The effect of crowding upon the oviposition of grain-infesting insects.' J. Exp. Biol. 19: 311–40.

Crombie, A. C. (1943). 'The effect of crowding upon the natality of grain-infesting insects.' Proc. Zool. Soc. Lond. A, 113: 77–98.

Crombie, A. C. (1944*a*). 'On intraspecific and interspecific competition in larvae of graminivorous insects.' J. Exp. Biol. 20: 135–51.

Crombie, A. C. (1944*b*). 'On the measurement and modification of the olfactory responses of blowflies.' J. Exp. Biol. 20: 159–66.

Crombie, A. C. (1944*c*). 'Rat plagues in western Queensland.' Nature, Lond. 154: 803–4.

Crombie, A. C. (1945). 'On competition between different species of graminivorous insects.' Proc. Roy. Soc. B, 132: 362–95.

Crombie, A. C. (1946). 'Further experiments on insect competition.' Proc. Roy Soc. B, 133: 76–109.

Cross, E. C. (1940). 'Periodic fluctuation in numbers of the red fox in Ontario.' J. Mammal. 21: 294–306.

Cutler, D. W. & Crump, L. M. (1920). 'Daily periodicity in the numbers of active soil flagellates: with a brief note on the relation of trophic amoebae and bacterial numbers.' Ann. Appl. Biol. 7: 11–24.

Cutler, D. W., Crump, L. M. & Sandon, H. (1922). 'A quantitative investigation of the bacterial and Protozoan population of the soil, with an account of the Protozoan fauna.' Philos. Trans. B, 211: 317–50.

D'Aeth, H. R. X. (1939). 'A survey of interaction between fungi.' Biol. Rev. 14: 105–31.

D'Ancona, U. (1942). 'La lotta per l'esistenza.' Torino.

Darlington, C. D. (1937). 'Recent advances in cytology.' 2nd ed. London.

Darlington, C. D. (1940). 'Taxonomic species and genetic systems.' In J. Huxley, 'The new systematics.' Pp. 137–60. Oxford.

Darwin, C. (1859). 'The origin of species by means of natural selection....' London.

Davies, W. (1928). 'The factor of competition between one species and another in seeds mixtures.' Welsh Plant Breeding Station, Ser. H, No. 8: 82–149.

Davis, M. B. (1945). 'The effect of population density on longevity in *Trogoderma versicolor* Creutz (= *T. inclusa* Lec.).' Ecology, 26: 353–62.

Diver, C. (1940). 'The problem of closely related species living in the same area.' In J. Huxley, 'The new systematics.' Pp. 303–28. Oxford.

Dobzhansky, T. (1941). 'Genetics and the origin of species.' Rev. ed. New York.

Edmondson, W. T. (1944). 'Ecological studies of sessile Rotatoria. Part I. Factors affecting distribution.' Ecol. Monogr. 14: 31–66.

Edmondson, W. T. (1945). 'Ecological studies of sessile Rotatoria. Part II. Dynamics of populations and social structures.' Ecol. Monogr. 15: 141–72.

Eisele, H. F. & Aikman, G. M. (1933). 'The development and survival of species and varieties in planted pastures.' Ecology, 14: 123–35.

Elson, P. F. (1942). 'Behavior and survival of planted Atlantic salmon fingerlings.' Trans. Seventh N. Amer. Wildlife Conf.: 202–7.

Elton, C. (1927). 'Animal ecology.' London.

Elton, C. (1930). 'Animal ecology and evolution.' Oxford.

Elton, C. (1933). 'The ecology of animals.' London.

Elton, C. (1942). 'Voles, mice and lemmings: problems in population dynamics.' Oxford.

Elton, C. (1944). 'Competition and the structure of animal communities.' Programme of a meeting of the British Ecological Society, 21 March 1944.

Elton, C. (1946). 'Competition and the structure of ecological communities.' J. Anim. Ecol. 15: 54–68.

Emerson, A. E. (1939*a*). 'Social co-ordination and the superorganism.' Amer. Midl. Nat. 21: 182–206.

Emerson, A. E. (1939*b*). 'Populations of social insects.' Ecol. Monogr. 9: 287–300.

Errington, P. L. (1946). 'Predation and vertebrate populations.' Quart. Rev. Biol. 21: 144–77, 221–45.

Evans, A. C. (1936). 'Studies on the influence of the environment on the sheep blow-fly *Lucilia sericata* Meig. IV. The indirect effect of temperature and humidity acting through certain competing species of blow-flies.' Parasitology, 28: 431–9.

Farrow, E. P. (1925). 'Plant life on East Anglian heaths....' Cambridge.

Fawcett, H. S. (1931). 'The importance of investigations on the effects of known mixtures of microorganisms.' Phytopathol. 21: 545–50.

Fisher, R. A. (1930). 'The genetical theory of natural selection.' Oxford.

Fisher, R. A., Corbet, A. S. & Williams, C. B. (1943). 'The relation between the number of species and the number of individuals in a random sample of an animal population.' J. Anim. Ecol. 12: 42–58.

Flanders, S. E. (1939). 'Environmental control of sex in hymenopterous insects.' Ann. Ent. Soc. Amer. 32: 11–26.

Flanders, S. E. (1942). 'Oösorption and ovulation in relation to oviposition in the Parasitic Hymenoptera.' Ann. Ent. Soc. Amer. 35: 251–66.

Flanders, S. E. (1945). 'The role of the spermatophore in the mass propagation of *Macrocentrus encylivorus*.' J. Econ. Ent. 38: 323–7.

Ford, J. (1937). 'Research on populations of *Tribolium confusum* and its bearing on ecological theory: a summary.' J. Anim. Ecol. 6: 1–14

Formosof, A. N. (1933). 'The crop of cedar nuts, invasions into Europe of the Siberian nutcracker (*Nucifraga caryocatactes macrorhynchus* Brehm) and fluctuations in numbers of the squirrel (*Sciurus vulgaris* L.).' J. Anim. Ecol. 2: 70–81.

Fuller, M. E. (1934). 'Insect inhabitants of carrion: a study in animal ecology.' Bull. Coun. Sci. Industr. Res. Aust. 82: 1–62.

Gagarin, B. (1933). Biol. Zh. Mook. 2: 451 (in Russian). [Cited by Bodenheimer (1938).]

Garrard, E. H. & Lockhead, A. G. (1938). 'Relationships between soil micro-organisms and soil-borne plant pathogens.' Sci. Agric. 18: 719–37.

Garrett, S. D. (1934). 'Factors affecting the pathogenicity of cereal foot-rot fungi.' Biol. Rev. 9: 351–61.

Garrett, S. D. (1938). 'Soil conditions and the root-infecting fungi.' Biol. Rev. 13: 159–85.

Garrett, S. D. (1939). 'Soil-borne fungi and the control of root disease.' Tech. Commun., Bur. Soil Sci. Harpenden, No. 38: 1–54.

Garrett, S. D. (1944). 'Root disease fungi.' Waltham, Mass.

Gause, G. F. (1932). 'The ecology of populations.' Quart. Rev. Biol. 7: 27–46.

Gause, G. F. (1934). 'The struggle for existence.' Baltimore.

Gause, G. F. (1935). 'Vérifications expérimentales de la théorie mathématique de la lutte pour la vie.' Actualités Sci. Industr. 277: 1–61.

Gause, G. F. (1936). 'The principles of biocoenology.' Quart. Rev. Biol. 11: 320–36.

Gause, G. F. (1937). 'Experimental populations of microscopic organisms.' Ecology, 18: 173–9.

Gause, G. F. (1942). 'The relation of adaptability to adaptation.' Quart. Rev. Biol. 17: 98–114.

Gause, G. F. & Witt, A. A. (1935). 'Behavior of mixed populations and the problem of natural selection.' Amer. Nat. 69: 596–609.

Gordon, C. (1939). 'A method for the direct study of natural selection.' J. Exp. Biol. 16: 278–85.

Graham, S. A. (1933). 'The influence of civilization on the insect fauna of North America. 1. The influence of civilization on the insect fauna of forests.' Ann. Ent. Soc. Amer. 26: 497–503.

Graham, S. A. (1939). 'Forest insect populations.' Ecol. Monogr. 9: 301–10.

Gray, J. (1929). 'The kinetics of growth.' Brit. J. Exp. Biol. 6: 248–74.

Greenwood, M., Hill, A. B., Topley, W. W. C. & Wilson, J. (1936). 'Experimental epidemiology.' Spec. Rep. Ser. Med. Res. Coun. 209: 1–204.

Hall, R. P. (1941*a*). 'Populations of plant-like flagellates.' Amer. Nat. 75: 419–37.

Hall, R. P. (1941*b*). 'Food requirements and other factors influencing growth of protozoa in pure cultures.' In G. N. Calkins & F. M. Summers, 'Protozoa in biological research', pp. 475–516. New York.

Hall, R. P. & Shottenfeld, A. (1941). 'Maximal density and phases of death in populations of *Glaucoma pirifoemis*.' Physiol. Zoöl. 14: 384–93.

Hamilton, G. E. H. Barrett- [& Hinton, M. A. C.] (1910–21). 'A history of British mammals.' London.

Hammond, E. C. (1938). 'Biological effects of population density in lower organisms.' Quart. Rev. Biol. 13: 421–38.

Hammond, E. C. (1939). 'Biological effects of population density in lower organisms (*concluded*).' Quart. Rev. Biol. 14: 35–59.

Hammond, J. (1941). 'Fertility in mammals and birds.' Biol. Rev. 16: 165–90.

Harvey, H. W. (1942). 'Production of life in the sea.' Biol. Rev. 17: 221–46.

Hering, M. (1926). 'Die Okologie der blattminierenden Insektenlarven.' Berlin.

L'Héritier, P. (1937). 'Étude de variations quantitatives au sein d'une espèce: *Drosophila melanogaster* Meig.' Arch. Zool. Exp. 78: 255–356.

L'Héritier, P. & Teissier, G. (1935). 'Recherches sur la concurrence vitale. Étude de populations mixtes de *Drosophila melanogaster* et *Drosophila funebris*.' C.R. Soc. Biol. 118: 1396–8.

L'Héritier, P. & Teissier, G. (1937). 'Elimination des formes mutantes dans les populations de Drosophiles. Cas des Drosophiles "Bar".' C.R. Soc. Biol. 124: 880–2. 'Cas des Drosophiles "ebony",' pp. 882–4.

Hinshelwood, C. N. (1944). 'Bacterial growth.' Biol. Rev. 19: 150–63.

Hinton, M. A. C. (1918). 'Rats and mice as enemies of mankind.' Brit. Mus. (Nat. Hist.) Econ. Ser. No. 8: 1–70.

Hogben, L. T. (1931). 'Some biological aspects of the population problem.' Biol. Rev. 6: 163–80.

Hogben, L. (1940). 'Problems of the origin of species.' In J. Huxley, 'The new systematics.' Pp. 269–86. Oxford.

Holdaway, F. G. (1930). 'Field populations and natural control of *Lucilia sericata*.' Nature, Lond. 126: 648–9.

Holman, W. L. (1928). 'Bacterial associations.' In E. I. Jordan & I. S. Falk, 'The newer knowledge of bacteriology and immunology.' Pp. 102–19. Chicago.

Howard, A. D. & Anson, B. J. (1922). 'Phases in the parasitism of the Unionidae.' J. Parasitol. 9: 68–82.

Huntington, E. (1931). 'The Matamek Conference on Biological Cycles, 1931.' Science, 74: 229–35.

Huntsman, A. G. (1941). 'Cyclical abundance and birds versus salmon.' J. Fish. Res. Bd. Canada, 5: 227–35.

Huskins, C. L. (1931). 'The origin of *Spartina Townsendii*.' Genetica, 12: 531–8.

Hutchinson, G. E. (1941). 'Ecological aspects of succession in natural populations.' Amer. Nat. 75: 406–18.

Huxley, J. S. (1940). 'Introductory: towards the new systematics.' In J. Huxley, 'The new systematics.' Pp. 1–46. Oxford.

Huxley, J. (1942). 'Evolution: the modern synthesis.' London.

Imms, A. D. (1937). 'Recent advances in entomology.' 2nd ed. London.

Jaccard, P. (1912). 'The distribution of the flora in the alpine zone.' New Phytol. 11: 37–50.

Jaccard, P. (1941). 'Sur le coefficient generique.' Chron. Bot. 6: 361–4.

Jackson, C. H. N. (1945). 'Comparative studies of the habitat requirements of tsetse fly species.' J. Anim. Ecol. 14: 46–51.

Jacobi, E. F. (1939). 'Über Lebensweise, auffinden des Wirtes und Regulierung der Individuenzahl von *Mormoniella vitripennis* Walker.' Arch. Néerl. Zool. 3: 197–282.

Jahn, T. L. (1934). 'Problems of population growth in the Protozoa.' Cold Spring Harbor Symp. Quant. Biol. 2: 167–80.

Jeffreys, H. (1917). 'On the vegetation of the four Durham Coal-measure fells. IV. On various other ecological factors.' J. Ecol. 5: 140–54.

Johnson, W. H. (1937). 'Experimental populations of microscopic organisms.' Amer. Nat. 71: 5–20.

Johnson, W. H. (1941). 'Populations of ciliates.' Amer. Nat. 75: 438–57.

Kendeigh, S. C. (1944). 'Measurement of bird populations.' Ecol. Monogr. 14: 67–106.

King, K. M. (1939). 'Population studies of soil insects.' Ecol. Monogr. 9: 270–86.

Kinsey, A. C. (1923). 'The gall wasp genus *Neuroterus* (Hymenoptera).' Ind Univ. Studies, 10: 1–150.

Kinsey, A. C. (1930). 'The gall wasp genus *Cynips*: a study in the origin of species.' Sci. Res. Pub. Waterman Inst. 42: 1–577.

Kostitzin, V. A. (1937). 'Mathematical biology.' Transl. from French by T. H. Savory. London, etc.

Kuczynski, R. R. (1935). 'The measurement of population growth.' London.

Lack, D. (1940). 'Habitat selection and speciation in birds.' Brit. Birds, 34: 80–4.

Lack, D. (1943). 'The life of the robin.' London.

Lack, D. (1944). 'Ecological aspects of species-formation in passerine birds.' Ibis, 86: 260–86.

Lack, D. (1945). 'The ecology of closely related species with special reference to cormorant (*Phalacrocorax carbo*) and shag (*P. aristotelis*).' J. Anim. Ecol. 14: 12–16.

Lack, D. (1946). 'Competition for food by birds of prey.' J. Anim. Ecol. 15: 123–9.

Lack, D. (1947). 'Darwin's finches.' Cambridge.

Laing, J. (1937). 'Host-finding by insect parasites. I. Observations on the finding of hosts by *Alysia manducator*, *Mormoniella vitripennis* and *Trichogramma evanescens*.' J. Anim. Ecol. 6: 298–317.

Laing, J. (1938). 'Host-finding by insect parasites. II. The chance of *Trichogramma evanescens* finding its hosts.' J. Exp. Biol. 15: 281–302.

Lal, A. (1939). 'Interaction of soil micro-organisms with *Ophiobolus graminis* Sacc., the fungus causing the take-all disease of wheat.' Ann. Appl. Biol. 26: 247–61.

Leslie, P. H. (1945). 'On the use of matrices in certain population mathematics.' Biometrika, 33: 183–212.

Lloyd, D. C. (1938). 'A study of some factors governing the choice of hosts and distribution of progeny by the Chalcid *Ooencyrtus kuvanae* Howard.' Philos. Trans. B, 229: 275–322.

Lloyd, D. C. (1940). 'Host selection by hymenopterous parasites of the moth *Plutella maculipennis* Curtis.' Proc. Roy. Soc. B, 128: 451–84.

Lloyd, L. (1943*a*). 'Materials for a study in animal competition. The fauna of the sewage bacteria beds. Part II.' Ann. Appl. Biol. 30: 47–60.

Lloyd, L. (1943*b*). 'Materials for a study in animal competition. III. The seasonal rhythm of *Psychoda alternata* Say and an effect of intraspecific competition.' Ann. Appl. Biol. 30: 358–64.

Lloyd, L., Graham, J. F. & Reynoldson, T. B. (1940). 'Materials for a study in animal competition. The fauna of the sewage bacteria beds.' Ann. Appl. Biol. 27: 122–50.

Lotka, A. J. (1925). 'Elements of physical biology.' Baltimore.

Lotka, A. J. (1932). 'The growth of mixed populations: two species competing for a common food supply.' J. Wash. Acad. Sci. 22: 461–9.

Lotka, A. J. (1934). 'Théorie analytique des associations biologiques. Première Partie. Principes.' Actualités Sci. Industr. 187: 1–45.

Lotka, A. J. (1939). 'Théorie analytique des associations biologiques. Deuxième Partie. Analyse démographique avec application particulière à l'espèce humaine.' Actualités Sci. Industr. 780: 1–149.

Lotka, A. J. (1945). 'Population analysis as a chapter in the mathematical theory of evolution.' In W. E. Le Gros Clark & P. B. Medawar, 'Essays on growth and form presented to D'Arcy Wentworth Thompson.' Pp. 355–85. Oxford.

Lucas, C. E. (1938). 'Some aspects of integration in plankton communities.' J. Cons. Int. Explor. Mer. 13: 309–22.

Lyell, C. (1830–33). 'The principles of geology.' 3 vols. London.

MacLagan, D. S. (1932). 'The effect of population density upon rate of reproduction with special reference to insects.' Proc. Roy. Soc. B, 111: 437–54.

MacLagan, D. S. (1940). 'Sunspots and insect outbreaks: an epidemiological study.' Proc. Univ. Durham Phil. Soc. 10: 173–99.

MacLagan, D. S. (1941). 'Recent animal-population studies; and their significance in relation to sociobiological philosophy (Part I).' Proc. Univ. Durham Phil. Soc. 10: 310–31.

MacLagan, D. S. & Dunn, E. (1935). 'The experimental analysis of the growth of an insect population.' Proc. Roy. Soc. Edin. 55: 126–39.

Malthus, T. R. (1798). 'An essay on population.' Reprinted 1926 with notes by James Bonar. London. ('An essay on the principle of population' republished in 'Everyman,' London, 1933.)

Martelli, G. (1907). 'Contribuzioni alla biologia della *Pieris brassica* L. e di alcuni suoi parassiti ed iperparassiti.' Boll. Lab. Zool. Portici, 1: 170–224.

Mason, D. T. (1915). 'The life history of the lodgepole pine in the Rocky Mountains.' Bull. U.S. Dep. Agric. 154: 1–35.

Mather, K. (1943). 'Polygenic inheritance and natural selection.' Biol. Rev. 18: 32–64.

Mayr, E. (1942). 'Systematics and the origin of species from the viewpoint of a zoologist.' New York.

Mell, R. & Heinrich, G. (1931). 'Beiträge zur Fauna Sinica. IX. Zur Biologie und Systematik der südchinesischen Ichneumoninae Ashm. (Fam. Ichneumonidae Hym.) Z. Angew. Ent. 18: 371–403.

Meyrick, E. [1928]. 'Revised handbook of British Lepidoptera.' London.

Morgan, T. H. & Tice, S. C. (1914). 'The influence of the environment on the size of expected classes.' Biol. Bull. Wood's Hole 26: 213–20.

Needham, J. G., Frost, S. W. & Tothill, B. H. (1928). 'Leaf-mining insects.' London.

Nicholson, A. J. & Bailey, V. A. (1935). 'The balance of animal populations. Part I.' Proc. Zool. Soc. Lond.: 551–98.

Nicol, H. (1934). 'Microbes in association.' Sci Progr. 29: 236–43.

Nicol, H. & Thornton, H. G. (1941). 'Competition between related strains of nodule bacteria and its influence on infection of the legume host.' Proc. Roy. Soc. B, 130: 32–59.

Noble, G. K. & Evans, G. (1932). 'Observations and experiments on the life history of the salamander, *Desmognathus fuscus fuscus* (Rafinesque).' Amer. Mus. Novi. 533: 1–16.

Olenov, J. M., Kharmac, I. S., Galkovskaja, K. T., Kniaževa, N. I., Lebedeva, A. D. & Popova, Z. T. (1937). 'Natural selection in wild *Drosophila melanogaster* populations.' C.R. Acad. Sci. U.R.S.S. 15: 97–9.

Park, T. (1937). 'Experimental studies of insect populations.' Amer. Nat. 71: 21–33.

Park, T. (1938). 'Studies in population physiology. VIII. The effect of larval population density on the post-embryonic development of the flour beetle, *Tribolium confusum* Duval.' J. Exp. Zool. 79: 51–70.

Park, T. (1939). 'Analytical population studies in relation to general ecology.' Amer. Midl. Nat. 21: 235–53.

Park, T. (1941). 'The laboratory population as a test of a comprehensive ecological system.' Quart. Rev. Biol. 16: 274–93, 440–61.

Park, T. (1942). 'Integration of infra-social insect populations.' Bio. Symposia, 8: 121–38.

Park, T. (1943). 'Inter-species competition within populations of the genus *Tribolium*.' Anat. Rec. 87: 462 (abstract).

Park, T., Gregg, E. V. & Lutherman, C. Z. (1941). 'Studies in population physiology. X. Interspecific competition in populations of granary beetles.' Physiol. Zoöl. 14: 395–430.

Park, T., Miller, E. V. & Lutherman, C. Z. (1939). 'Studies in population physiology. IX. The effect of imago population density on the duration of the larval and pupal stages of *Tribolium confusum* Duval.' Ecology, 20: 365–73.

Parker, D. L. (1933). 'The interrelations of two Hymenopterous egg parasites of the gipsy moth, with notes on the larval instars of each.' J. Agric. Res. 46: 23–34.

Pavlychenko, T. K. & Harrington, J. B. (1934). 'Competitive efficiency of weeds and cereal crops.' Canad. J. Res. 10: 77–94.

Pearl, R. (1922). 'The biology of death.' Philadelphia etc.

Pearl, R. (1925). 'The biology of population growth.' New York.

Pearl, R. & Miner, J. R. (1935). 'Experimental studies on the duration of life. XIV. The comparative mortality of certain lower organisms.' Quart. Rev. Biol. 10: 60–79.

Pearse, A. S. (1939). 'Animal ecology.' New York, etc.

Picard, F. (1922). 'Contribution à l'étude des parasites de *Pieris brassicae* L.' Bull. Biol. 56: 54–130.

Porter, C. L. & Carter, J. C. (1938). 'Competition among fungi.' Bot. Rev. 4: 165–82.

Prenant, M. (1934). 'Adaptation, écologie et biocoenotique.' Actualités Sci. Industr. 103: 1–59.

Rasmussen, D. I. (1941). 'Biotic communities of Kaibal Plateau, Arizona.' Ecol. Monogr. 11: 229–98.

Régnier, J. & Lambin, S. (1934). 'Étude d'un cas d'antagonisme microbien (*B. coli-Staphylococcus aureus*).' C.R. Acad. Sci. 199: 1682–4.

Reynolds, J. M. (1944). 'The biology of *Tribolium destructor* Uytt. I. Some effects of fertilization and food factors on fecundity and fertility.' Ann. Appl. Biol. 31: 132–42.

Reynoldson, T. B. (1942). 'Further studies on the biology of a double filtration plant at Huddersfield.' J. Proc. Inst. Sewage Purif.: 3–22.

Ribbands, C. R. (1944). 'The influence of rainfall, tides and periodic fluctuations on a population of *Anopheles melas* Theo.' Bull. Ent. Res. 35: 271–95.

Richards, O[scar] W. (1934). 'The analysis of growth as illustrated by yeast.' Cold Spring Harbor Symp. Quant. Biol. 2: 157–66.

Richards, O[scar] W. (1941). 'The growth of the Protozoa.' In G. N. Calkins & E. M. Summers, 'Protozoa in biological research.' Pp. 517–64. New York.

Richards, O[wen] W. (1927). 'Sexual selection and allied problems in the insects.' Biol. Rev. 2: 298–364.

Rivnay, E. (1938). 'Factors affecting the fluctuations in the population of *Toxoptera aurantii* Boy. in Palestine.' Ann. Appl. Biol. 25: 143–54.

Robertson, F. W. & Sang, J. H. (1944*a*). 'The ecological determinants of population growth in a *Drosophila* culture. I. Fecundity of adult flies.' Proc. Roy Soc. B, 132: 258–77.

Robertson, F. W. & Sang. J. H. (1944*b*). 'The ecological determinants of growth in a *Drosophila* culture. II. Circumstances affecting egg viability.' Proc. Roy. Soc. B, 132: 277–91.

Robson, G. C. (1928). 'The species problem....' Edinburgh, etc.

Robson, G. C. & Richards, O. W. (1936). 'The variation of animals in nature.' London.

Rübel, E. (1935). 'The replaceability of ecological factors and the law of the minimum.' Ecology, 16: 336–41.

Russell, E. J. (1937). 'Soil conditions and plant growth.' 7th ed. London.

Russell, E. S. (1941). 'Biological adaptedness and specialization of instinctive behaviour.' Proc. Linn. Soc. 153: 250–68.

Russell, E. S. (1942). 'The overfishing problem.' Cambridge.

Salisbury, E. J. (1929). 'The biological equipment of species in relation to competition.' J. Ecol. 17: 197–222.

Salisbury, E. J. (1940). 'Ecological aspects of plant taxonomy.' In J. Huxley, 'The new systematics.' Pp. 329–40. Oxford.

Salt, G. (1934). 'Experimental studies in insect parasitism. II. Super-parasitism.' Proc. Roy. Soc. B, 114: 455–76.

Salt, G. (1937). 'The sense used by *Trichogramma* to distinguish between parasitized and unparasitized hosts.' Proc. Roy. Soc. B, 122: 57–75.

Salt, G. (1941). 'The effects of hosts upon their insect parasites.' Biol. Rev. 16: 239–64.

Saunders, A. M. Carr- (1922). 'The population problem: a study in human evolution.' Oxford.

Saunders, A. M. Carr- (1936). 'World population: past growth and present trends.' Oxford.

Severtzoff, S. A. (1934). 'On the dynamics of populations of vertebrates.' Quart. Rev. Biol. 9: 409–37.

Severtzoff, S. A. (1941). 'Population dynamics and adaptive evolution of animals.' Moscow Acad. Sci. U.S.S.R. (In Russian: Reviewed by B. P. Uvarov (1944) in Nature, Lond. 153: 66–7.)

Shelford, V. E. (1911). 'Ecological succession. III. A reconaissance of its causes in ponds with particular reference to fish.' Biol. Bull. Woods Hole, 22: 1–38.

Shelford, V. E. & Flint, W. P. (1943). 'Populations of the cinch bug in the Upper Mississippi Valley from 1823–1940.' Ecology, 24: 435–55.

Singh, B. N. (1942). 'Selection of bacterial food by soil flagellates and amoebae.' Ann. Appl. Biol. 29: 18–22.

Sladen, F. W. L. (1912). 'The humble-bee.' London.

Smith, H. S. (1933). 'The influence of civilization on the insect fauna of North America. IV. The influence of civilization on the insect fauna by purposeful introductions.' Ann. Ent. Soc. Amer. 26: 518–28.

Smith, H. S. (1935). 'The role of biotic factors in the determination of population densities.' J. Econ. Ent. 28: 873–98.

Smith, H. S. (1939). 'Insect populations in relation to biological control.' Ecol. Monogr. 9: 311–20.

Stanley, J. (1941). 'A mathematical theory of the growth of populations of the flour beetle *Tribolium confusum* Duv. IV. A modified theory descriptive of the relation between the limiting value of egg-populations in the absence of hatching, and the volume (or weight) of flour used in the culture.' Ecology, 22: 23–37.

Stanley, J. (1942). 'A mathematical theory of the growth of populations of the flour beetle *Tribolium confusum* Duv. V. The relation between the limiting value of egg-populations in the absence of hatching and the sex-ratio of the group of adult beetles used in a culture.' Ecology, 23: 23–31.

Stanley, J. (1943). 'A mathematical theory of the growth of populations of the flour beetle *Tribolium confusum* Duv. VI. Egg populations in which the initial number of eggs is above the limiting value.' Ecology, 24: 323–8.

Stapledon, R. G. (1928). 'Cocksfoot grass (*Dactylis glomerata* L.): ecotypes in relation to the biotic factor.' J. Ecol. 16: 71–104.

Stapledon, R. G. & Davies, W. (1928). 'Seeds mixture experiments with special reference to the influence of environmental factors.' Welsh Plant Breeding Station, Ser. H, No. 8: 7–81.

Strangeland, C. E. (1904). 'Pre-Malthusian doctrines of population.' Columbia Univ. Studies in History, Economics and Public Law, XXI, No. 3.

Sukatschew, W. (1928). 'Einige experimentelle Untersuchungen über den Kampf ums Dasein zwischen Biotypen derselben Art.' Z. Indukt. Abstamm- u. VererbLehre 47: 54–74.

Taliaferro, W. H. (1941). 'Populations of blood-dwelling species.' Amer. Nat., 75: 458–72.

Tansley, A. G. (1917). 'On competition between *Galium saxatile* L. (*G. Hercynicum* Weig.) and *Galium sylvestre* Poll. (*G. Asperum* Schreb.) on different types of soil.' J. Ecol. 5: 173–9.

Tansley, A. G. (1939). 'The British Islands and their vegetation.' Cambridge.

Thompson, D'A. W. (1942). 'On growth and form.' Cambridge.

Thompson, W. R. (1939). 'Biological control and the theories of the interactions of populations.' Parasitology, 31: 299–388.

Thompson, W. R. (1943–45). 'A catalogue of the parasites and predators of insect pests.' Belleville, Ont., Canada.

Thompson, W. S. (1942). 'Population problems.' New York.

Thomson, G. M. (1922). 'The naturalization of animals and plants in New Zealand.' Cambridge.

Thorpe, W. H. (1930). 'Biological races in insects and allied groups.' Biol. Rev. 5: 177–212.

Thorpe, W. H. (1940). 'Ecology and the future of systematics.' In J. Huxley, 'The new systematics.' Pp. 341–64. Oxford.

Thorpe, W. H. (1943*a*). 'Types of learning in insects and other arthropods, Part I.' Brit. J. Psychol. 33: 220–34.

Thorpe, W. H. (1943*b*). 'Types of learning in insects and other arthropods, Part II.' Brit. J. Psychol. 34: 20–31.

Thorpe, W. H. (1944*a*). 'Types of learning in insects and other arthropods, Part III.' Brit. J. Psychol. 34: 66–76.

Thorpe, W. H. (1944*b*). 'Some problems of animal learning.' Proc. Linn. Soc. Lond. 156: 70–83.

Thorpe, W. H. (1945). 'The evolutionary significance of habitat selection.' J. Anim. Ecol. 14: 67–70.

Thorpe, W. H. & Caudle, H. B. (1938). 'A study of the olfactory responses of insect parasites to the food plant of their hosts.' Parasitology, 30: 523–8.

Timoféeff-Ressovsky, N. W. (1933). 'Über die relative Vitalität von *Drosophila melanogaster* Meigen und *Drosophila funebris* Fabricius (Diptera Muscidae acalypteratae) unter verschiedenen Zuchtbedingungen, in Zusammenhang mit den Verbreitungsarealen dieser Arten.' Arch. Naturgesch. 2: 285–90.

Timoféeff-Ressovsky, N. W. (1935). 'Über geographische Temperaturrassen bei *Drosophila funebris* F.' Arch. Naturgesch. 4: 245–57.

Timoféeff-Ressovsky, N. W. (1940). 'Mutations and geographical variation.' In J. Huxley, 'The new systematics.' Pp. 73–136. Oxford.

Topley, W. W. C. (1926). 'The first [second] [third] (1926) Milroy lecture on experimental epidemiology.' Lancet 210: 477–84, 531–7, 645–51.

Topley, W. W. C. (1942). 'The Croonian lecture: The biology of epidemics.' Proy. Roy. Soc. B, 130: 337–59.

Turrill, W. B. (1931). 'Biological races in seed-bearing plants and their significance in evolution.' Ann. Appl. Biol. 18: 442–50.

Turrill, W. B. (1940). 'Experimental and synthetic plant taxonomy.' In J. Huxley, 'The new systematics.' Pp. 47–71. Oxford.

Ullyett, G. C. (1936). 'Host selection by *Microplectron fuscipennis*, Zett. (Chalcididae, Hymenoptera).' Proc. Roy. Soc. B, 120: 253–91.

Uvarov, B. P. (1931). 'Insects and climate.' Trans. R. Ent. Soc. Lond. 79: 1–247.

Varley, G. C. (1941). 'On the search for hosts and the egg distribution of some chalcid parasites of the knapweed gall-fly.' Parasitology, 33: 47–66.

Vestal, A. G. (1914). 'Internal relations of terrestrial associations.' Amer. Nat. 48: 413–45.

Vevers, H. G. (1938). 'Review of recent ecological literature.' Bull. Anim. Behav. 1, No. 1: 2–7.

Vevers, H. G. (1939). 'Experimental populations.' Bull. Anim. Behav. 1, No. 2: 1–5.
Vladimerova, M. S. & Smirnov, E. S. (1938). Meditsinskaia Parazitologiia i Parazitarnye Bolezni (Med. Parasitol. and Parasitic Dis.). 7, No. 5: 755–77. [Biol. Abstr. 14: 753, entry 8066.]
Volterra, V. (1926). 'Variazioni e fluttuazioni del numero d'individui in specie animali conviventi.' Mem. Accad. Lincei, 2: 31–113. (Transl. as Appendix to Chapman 1931.)
Volterra, V. & D'Ancona, U. (1935). 'Les associations biologiques au point de vue mathématique.' Actualités Sci. Industr. 243: 1–97.
Voûte, A. D. (1943). 'Classification of factors influencing the natural growth of a population of insects.' Acta Biotheoretica, 1; 99–116.
Waksman, S. A. (1937). 'Associative and antagonistic effects of micro-organisms: I. Historical review of antagonistic relationships.' Soil Sci. 43: 51–68.
Warming, E. & Vähl, M. (1909). 'Oecology of plants: an introduction to the study of plant-communities.' Oxford.
Weindling, R. (1938). 'Association effects of fungi.' Bot. Rev. 4: 475–96.
White, B., Robinson, E. S. & Barnes, L. A. (1938). 'The biology of pneumococcus.' New York.
Wilder, J. (1940). 'The effects of population density upon growth reproduction, and survival of *Hyalella azteca*.' Physiol. Zoöl. 13: 439–61.
Wilkes, A. (1942). 'The influence of selection on the preferendum of a chalcid (*Microplectron fuscipennis* Zett.), and its significance in the biological control of an insect pest.' Proc. Roy. Soc. B, 130: 400–15.
Williams, R. H. (1941). 'Growth-promoting nutrilites for yeasts.' Biol. Rev. 16: 49–80.
Wilson, E. A. (1907). 'Mammalia (whales and seals).' In National Antarctic Expedition 1901–4, Nat. Hist. 2: 1–69. London.
Wilson, C. B. (1917). 'Copepod parasites of freshwater fishes and their economic relations to mussel glochidia.' Bull. U.S. Bur. Fish. 34: 331–74.
Woodruff, L. L. (1912). 'Observations on the origin and sequence of the protozoan fauna of hay infusions.' J. Exp. Zool. 12: 205–64.
Woodruff, L. L. (1914). 'The effect of excretion products of infusoria on the same and on different species, with special reference to protozoan sequence in infusions.' J. Exp. Zool. 14: 575–82.
Wright, S. (1940). 'The statistical consequences of Mendelian heredity in relation to speciation.' In J. Huxley, 'The new systematics.' Pp. 161–84. Oxford.
Zobell, C. E. (1946). 'Marine microbiology: A monograph on hydrobacteriology.' Waltham, Mass.

ADDENDUM (see p. 59)

Dr Park has kindly given me permission to mention some results of his large-scale study of competition between *Tribolium confusum* and *T. castaneum* which bear on the subject of this paper. When living alone each species does well in the medium used, but in competition they never survive together in equilibrium. When both species are infected with the protozoan parasite *Adelina tribolii*, *Tribolium confusum* usually eliminates its rival, although sometimes the reverse occurs. With *Adelina*-free insects, *T. castaneum*, whose single-species populations are the more reduced by this parasite, was more frequently the survivor. These results should be consulted in detail when they are published.

PERIODIC FLUCTUATIONS IN THE PREVALENCE OF THE WHEAT BLOSSOM MIDGES

By H. F. BARNES, *Rothamsted Experimental Station*

(With 1 Figure in the Text)

In 1932 it was suggested (1932*b*) that there might be regular fluctuations in numbers of the wheat blossom midges (*Sitodiplosis mosellana* Géhin and *Contarinia tritici* Kirby) and that such cycles might have their peaks about every fourth, fifth or sixth year. This hypothesis was based on the observations made by reporters of the Ministry of Agriculture and the writer's study of the two species involved on the field of permanent wheat (Broadbalk) at the Rothamsted Experimental Farm, Harpenden, over the years 1927–31. Later (1934), a graph was published showing the suggested rhythmic fluctuations. In this the peak years of abundance based on the observations were 1916, 1920 and 1926, while 1931 was the peak year determined by the Broadbalk study and the year 1937 was suggested as the next peak year of abundance.

Detailed accounts of the study on Broadbalk covering the years 1927–40 have already appeared (1932*a*, 1941). In addition, shorter papers concerning the prolonged larval life and the resultant delayed emergence of the midges (1943) and concerning the close interrelationships of the midges and their host plant (1944) have been published. The latter fact has made available a useful first estimate of the crop yield, while regarding the former sufficient data have now accumulated for it to be stated that the larvae of *Sitodiplosis mosellana* can emerge successfully after spending seven winters in the soil and those of *Contarinia tritici* after three.

Table 1. *Prevalence of the wheat blossom midges* (Contarinia tritici *and* Sitodiplosis mosellana) *on Broadbalk*, 1927–46

	No. of larvae present in 500 ears of wheat			Percentage grain attack		
Year	*C. tritici*	*S. mosellana*	Both species	*C. tritici*	*S. mosellana*	Both species
1927	1,780	715	2,495	0·95	2·2	3·2
1928	2,195	2,043	4,238	0·79	5·7	6·5
1929	19,265	587	19,852	5·9	1·8	7·7
1930	18,595	3,746	22,341	5·9	11·7	17·6
1931	19,273	6,027	25,300	6·4	15·0	21·4
1932	7,356	3,114	10,470	5·0	10·8	15·8
1933	1,474	319	1,793	0·7	1·4	2·1
1934	3,362	572	3,934	1·5	2·5	4·0
1935	4,297	4,226	8,523	2·1	17·9	20·0
1936*	708	2,872	3,580	0·5	9·2	9·7
1937	2,555	3,420	5,975	1·7	13·9	15·6
1938	378	827	1,205	0·2	3·2	3·4
1939	1,116	1,615	2,731	0·7	9·1	9·8
1940	977	2,291	3,268	1·1	7·5	8·6
1941	522 (2,297†)	2,736	3,258 (5,033†)	0·99	10·3	11·3
1942	1,143 (2,286†)	2,064	3,207 (4,350†)	0·96	7·9	8·9
1943	1,880	2,363	4,243	0·82	9·6	10·4
1944	1,030 (2,060†)	133	1,163 (2,193†)	0·98	0·53	1·5
1945	24,643	3,557	28,200	6·8	11·0	17·8
1946	29,638	3,853	33,491	13·3	13·3	26·6

* See p. 75.

† Estimated peak number of larvae, based on a study of the descent of the larvae to the soil from the wheat ears. This has been studied each year since 1941, but corrections are not necessary for 1943, 1945 or 1946 and in no year for *S. mosellana*.

It is hoped to publish the full data obtained subsequent to 1940 in due course. This will contain information concerning an improved method of determining the correct date on which to sample the wheat, which involves a study of the descent of the larvae from the wheat ears to the soil.

But since there are data available for twenty consecutive years, it is considered appropriate to draw attention now to the manner in which the suggested fluctuations in numbers have actually taken place. The accompanying Table 1 gives the numbers of the larvae of the two species, separately

and together, found in 500 ears of wheat from 1927–46 inclusive, as well as the corresponding percentage grain attack. Fig. 1 indicates the peak years of the wheat blossom midges as observed previous to 1927 and the total numbers of larvae found in the Broadbalk investigation during the years 1927–46. Both species of midges are considered together so as to fit in with the previous observations. It has already been pointed out (1941) that the year 1936 was exceptional both for the abnormal precipitation and subsequent hot weeks which may have been responsible for the unexpected decrease in numbers of larvae as well as for the fact that the effects of manurial treatments and so on on the Rothamsted wheat figures on Broadbalk field were strange as a whole in that year although other fields on the same farm gave normal results.

It can be seen that there have been two large peaks, in 1931 and in 1946, as well as two minor peaks, in 1935 (?1936) and in 1941. These fit in well with the original hypothesis that the midges might have rhythmic fluctuations in numbers with peaks every fourth, fifth or sixth year, and corresponding troughs. The latter have occurred in 1927, 1933, 1938 and 1944. The two species considered separately show the same rhythmic rise and fall, the peak and trough years for *Contarinia tritici* and *Sitodiplosis mosellana* being practically identical. The study is being continued and it is to be hoped that its continuance will soon cease to be dependent on one person carrying it out.

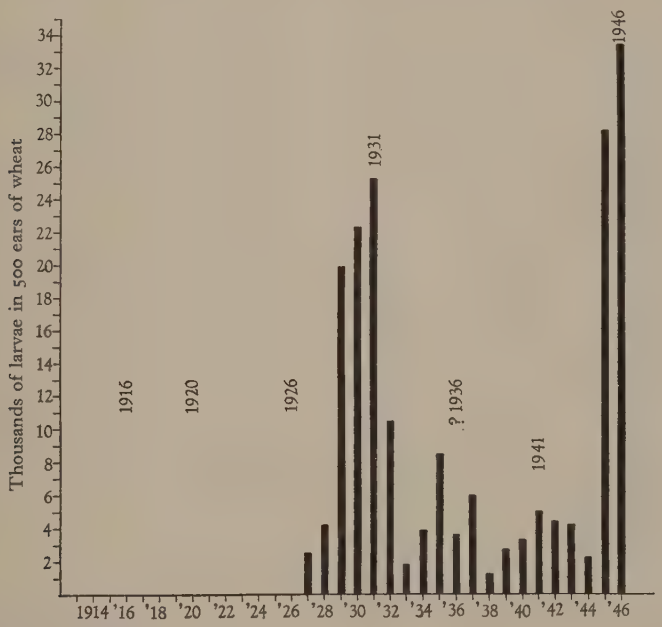

Fig. 1. Numbers of wheat blossom midges (*Contarinia tritici* and *Sitodiplosis mosellana*) in 500 ears of wheat.

REFERENCES

Barnes, H. F. (1932*a*). 'Studies of fluctuations in insect populations. I. The infestation of Broadbalk wheat by the wheat blossom midges (Cecidomyidae).' J. Anim. Ecol. 1: 12–31.

Barnes, H. F. (1932*b*). 'Periodic fluctuations in the prevalence of the wheat blossom midges.' J. Anim. Ecol. 1: 191–2.

Barnes, H. F. (1934). 'Sudden outbreaks of insect pests.' J. S.-E. Agric. Coll. Wye, no. 34: 260–8.

Barnes, H. F. (1941). 'Studies of fluctuations in insect populations. VIII. The wheat blossom midges on Broadbalk, 1932–40, with a discussion of the results obtained 1927–40.' J. Anim. Ecol. 10: 94–120.

Barnes, H. F. (1943). 'Studies of fluctuations in insect populations. X. Prolonged larval life and delayed subsequent emergence of the adult gall midge.' J. Anim. Ecol. 12: 137–8.

Barnes, H. F. & Weil, J. W. (1944). 'Studies of fluctuations in insect populations. XI. The interrelationship of the wheat blossom midges and their host plant.' Ann. Appl. Biol. 31: 231–4.

ESSAY REVIEW

THE SOIL FAUNA: WITH SPECIAL REFERENCE TO THE ECOSYSTEM OF FOREST SOIL

By G. R. FENTON

(With 2 Figures in the Text)

1. INTRODUCTION

The work recorded here was originally undertaken to meet one of the requirements for a B.A. in Forestry at Oxford. As first conceived, the work covered a much larger field than the present article, though in less detail, and included experimental work carried out with Ladell's apparatus (Ladell, 1936) very kindly lent by Dr C. B. Williams of Rothamsted Experimental Station. Owing to unexpected circumstances it was found possible to continue the work after the completion of the degree course. I owe much during this further period of work to the ever-ready help and encouragement of Mr Charles Elton, Prof. H. G. Champion and Dr R. N. Chrystal. I am also extremely indebted to Dr B. M. Hobby for checking back to original sources nearly all my references, after my departure from England.

The first section of this paper is intended as a comprehensive review of the methods so far used in sampling the soil population quantitatively, together with methods from other fields which have obvious application to the study of the soil fauna. The second part, however, makes no pretence at completeness; rather it is a collection of ideas brought together from diverse sources in an attempt to envisage the interrelations of plant and animal in the soil. The role of the animals is stressed and considered in particular relation to the two temperate soil types, podsol and Brown Forest Soil. No attempt has been made to catalogue the soil animals and discuss their effects on the soil group by group, as this aspect of the work has already been adequately treated in the papers of Taylor (1930, 1935) and Jacot (1940).

The bibliography covers a much wider field than does the text, and though no claim is made for more than an introduction to such fields as agricultural pests and mycorrhiza, the relation of soil animals to forest soils and the methods of assessing the soil population are covered as completely as possible.

2. TECHNIQUES EMPLOYED IN ASSESSING THE SOIL POPULATION

Defining soil animals as those which, at one time or another, in the course of their development or as adults, live within or beneath the soil surface, we are confronted with an array of animals ranging from bacteria to badgers. This animal range may be divided into three size classes, each with its own necessary sampling techniques. The smallest, the microfauna, ranges in size from 1 to 40 μ, and includes bacteria, Protozoa, Rotifera, the smaller species and larvae of nematodes, and small mites. The next subdivision, the mesofauna, includes creatures just visible with a hand lens, and at the other extreme those several centimetres long belonging to the Enchytraeidae, Nematoda, Acarina, Annelida, Crustacea, Myriapoda, Arachnida, Gastropoda, and Insecta. Finally, there is the macrofauna consisting largely of vertebrates such as toads, lizards, snakes, rodents, moles, etc.

(*a*) *Microfauna* (*bacteria and Protozoa*). Cultural methods as used in medical practice give assessments which are too low owing to the fact that some of the species are non-sporulating forms. For the bacteria, Waksman (1927) quotes Winogradsky's dilution technique (1925, 1933) combined with direct fixation as a method of giving more accurate counts. In the case of the Protozoa, Sandon (1927) describes a culture technique combined with identification of living Protozoa as the best method of assessing the population of these animals. The difficulty with Protozoa lies in the fact that many species require as food particular species of bacteria (Singh, 1941), whilst others do not encyst and thus are readily killed off.

Cobb (1918) made an extensive survey of the nematode population, using a technique somewhat as follows:

1. The soil sample is gently stirred with an appropriate volume of water when sand and other coarse and heavy material settles to the bottom.

2. The supernatant liquid is decanted and washed through a series of sieves, the finest being made of millers' or bolting silk.

3. The animals are washed off the sieves with the minimum quantity of water into a watch-glass and examined directly, the nematodes being removed with very fine needles.

(*b*) *Mesofauna.* If we add to the techniques already used in population studies of the soil mesofauna others of obvious application but so far only used in separating animals from foodstuffs, we can classify them into the following categories: (1) Direct sorting, (2) Sieving, (3) Flotation, (4) Automatic, (5) Centrifuging, and (6) Wetting methods.

The first method is the simplest, but most laborious, and was soon abandoned except in the case of the larger animals. It has been employed during the war in a wireworm census of Great Britain (Miles & Cohen, 1939; Miles, 1945). One of the earliest sieving techniques published was that devised by Morris (1920, 1922), which was simply to wash the soil through a series of sieves. Another method, used in America, employed a pair of sieves mechanically rotated the one within the other. This method was used for sorting large volumes of soil which were gradually fed into the machine (Lane & Shirck, 1938).

The idea of flotation first used by Daniels in his apparatus for counting potato flea larvae was later developed by Ladell (1936) who used a solution of magnesium sulphate in water, sp.gr. 1·11, as a non-toxic medium in which to float the insects. The solutions of sodium chloride and magnesium sulphate have the further advantage that they break down the structure of the soil and so liberate the smaller animals. In Ladell's apparatus a stream of bubbles further breaks up the soil, and also facilitates the rise of the insects to the top of the liquid.

With the flotation methods the final catch consists of vegetable litter and animals. The large volume of debris obtained from conifer sites with a pronounced litter layer constitutes one of the major difficulties in assessing the population of such soils. Salt & Hollick (1944) have recently developed a technique for 'separating' animal from plant material by the use of such liquids as benzene, toluene, etc., which have the property of wetting chitin but not vegetable matter. The organic liquid is poured on to the suspension of plant and animal material floating in the magnesium sulphate solution. The whole is then agitated by an air-jet and again allowed to settle. Under these conditions the animals come to rest on top of the benzene-water interface with the plant material below it. These principles have been applied by Strickland (1945) in his work on the soil fauna of forest and cacao plantations in Trinidad. In order to get rid of the litter Strickland boiled the suspension of litter and animals before adding kerosene, thus expelling air from the vegetable matter and allowing it to sink, and at the same time killing the arthropods in an extended state. Strickland states that if much vegetation is present three or four applications of kerosene and considerable stirring are necessary to detach all the smaller mites. With the large quantities of vegetable debris present in coniferous soils the difficulty of washing the debris adequately becomes a serious weakness of the method

The method described by Salt & Hollick, of counting wireworm larvae on the surface of a benzene-water interface has been found by the author, in preliminary tests not recorded here, to be unsatisfactory for accurate counts of the smaller nymphal and adult mites. The chief sources of error in making accurate counts are: (1) The pronounced curved surface at the liquid-glass contact, which results in such a concentration of debris and animals round the edge of the vessel that accurate counting is impossible; (2) the use of a grid to facilitate counting and ensure that no animals are counted twice is precluded by the curved surface of the liquid, the underlying mass of debris, and the depth of water beneath the benzene.

In order to count the catch accurately some method of spreading it uniformly over a flat surface is most desirable. This may be done by catching the animals on a marked filter paper (Ford, 1936) or transferring them to a shallow glass dish with vertical walls containing a liquid in which the animals will sink. A blue background on which is ruled a grid may then be placed beneath the vessel. The grid should be of such a size that one square just fits into the field of view of the binocular microscope used for counting.

An alternative method of extracting the fauna is known as the automatic method. Berlese (1905) developed this technique, which depends upon the fact that animals move downwards when the soil is desiccated. In a Berlese funnel the sample is supported on a sieve through which the animals pass when the sample is desiccated, to fall into a smooth funnel and thence into a phial of fixative. This method was further developed by Tullgren (1917), who used an electric lamp as a source of both heat and light, thus combining the negative phototrophic response of the animals with their reaction to desiccation in driving them downwards. The danger of this apparatus is that if the desiccation proceeds too rapidly the animals die before they can escape. Trägårdh (1933) has investigated this method in detail and criticized the work of Bornebusch (1940) on the grounds that he desiccated his material too rapidly and at too high a temperature. Trägårdh's own work is perhaps to be criticized in that his conclusions are based on rather few samples. One further point that Trägårdh brings out in his criticism of Bornebusch's work is the importance of the background against which the animals are examined. No critical study of this point is known to the author, but both Jacot (1936*b*, *c*) and Trägårdh (1933) state that dark blue backgrounds are more effective than white ones. It is interesting to note that Dammerman (1925, 1937) considers the automatic method less applicable to tropical soils than temperate ones owing to the fact that tropical forms tend to encyst or become torpid under the influence of desiccation, rather than leave the soil. In addition to the methods already described, Solomon (1945) separated mites from flour by shaking the whole with ethylene dichloride, sp.gr. 1·25; after the vessel was left to

stand, the mites rose to the surface and were easily floated on to a filter paper by the addition of more ethylene dichloride.

Yet another method for separating mites from flour has been elaborated by Russian workers. The basic principle of Shchastny's (1939) and Smirnov's (1938) methods is that the animals are separated from the flour by centrifugal force. In Shchastny's method the flour and mites are first treated with alcohol and then centrifuged. The centrifugate is then treated with a mixture of sodium chloride and glycerol solutions in equal proportions, stirred and again centrifuged. Under this treatment the mites and eggs rise to the surface of the liquid. Smirnov treated 10 g. of flour with 200 c.c. of antiformin, centrifuged and examined the centrifugate for mites and eggs.

The last method, i.e. using a wetting solution to wash out mites from organic matter, has been developed by Thomas & Horsfall (1939) who used 10% aqueous solution of Vatsol O.T. to wash out the mites, etc. from the manure.

So far the methods described may be termed direct in that they imply taking a sample of the soil, and after extracting the population so far as is possible by the method used, identifying, counting and then mathematically computing the population of the universe sampled. There remains, however, the indirect method, characteristically used for the macrofauna, but applied to the mesofauna by Bryson (1939). In this case the typical burrows of the various insects were identified, and subsequently used as the basis of a survey of the insect population.

The use of chemicals, either as irritants poured upon the soil or as attractive baits, has been particularly exploited at Rothamsted. Barnes (1941) carried out a survey of *Tipula paludosa* using an emulsion of orthodichlorobenzene and Jeyes Fluid which was applied to the soil at the rate of 1 gal./sq.yd. The animals react to this substance by coming to the surface, but if a census is to be carried out the animals must be collected immediately or they reburrow into the ground after the lapse of a few minutes. Such a method is only accurate for the larger larvae and even for these it is very probable that the whole population is not brought to the surface. A similar method is recommended for the collection of earthworms, though here the solution suggested is potassium permanganate. Metaldehyde has also been used by Barnes & Weil (1942) as a poisonous bait to get sample kills of the slug population of horticultural plots.

(*c*) *Macrofauna.* Owing to the size, mobility and relatively low density per acre of rodents and other small mammals, indirect methods have been used to estimate populations of them. The methods employed have been either those of trapping or baiting over the whole, or part, of the area; or alternatively of estimating the number of animals from counts of inhabited burrows or pellets.

A brief consideration of the problem of assessing the 'total' population shows that it falls into two parts. First, the technique of extracting and identifying the animals concerned, and secondly, the size and number of samples required for estimating the population within some stated limits of error. So far we have covered the methods used in extracting the mesofauna of the soil. It remains, however, to point out that these methods do not sample the different sections of the community with the same degree of accuracy and that in order to obtain the nearest approach to the 'true' population we must use the maximum number of each group of animals taking into consideration the results obtained from the whole range of methods.

Turning now to the size of samples it may be stated that it should be such that numerically large and zero counts are avoided. It is obvious, considering the mesofauna alone, that in order to assess correctly the populations of the Thysanura, Collembola, and small Acarina a considerable range of sample sizes would be required. Up to the present this has not been attempted, each author having arbitrarily selected his own sample size. Similar considerations have influenced the choice of magnification used for counting, with the result that one author covers large areas with a low power and arrives at quite a different estimate of the population from another worker using a high power and covering a smaller area. Anyone who has worked in this field will realize that these are practical compromises, but none the less they are sources of error. This point is well brought out by Trägårdh (1933) in the comparison of his own work with that of Bornebusch. Thus, to obtain the maximum number of animals using a given technique, consideration must be given to the optimum size of sample and to the magnification used in counting the sample. Jones (1937) discusses from a statistical point of view the size and number of samples required to give a reliable wireworm population figure per acre using a soil-sifting machine. He concludes that twenty-five 1 sq.ft. samples are adequate and equivalent to fifty $\frac{1}{4}$ sq.ft. samples or one hundred $\frac{1}{10}$ sq.ft. samples. For the bacteria and Protozoa samples from $\frac{1}{2}$–4 cu.in. have been considered adequate, whilst the usual size of sample for the mesofauna is from 20 to 30 cu.in.

Before closing this section on samples and sampling technique, it should be stressed that the determination of soil populations is only the first step in the solution of the problems of pest control and litter decomposition which must, if the results are not to be sterile, be followed by investigations of the physiology and ecology of the animals concerned.

3. THE RELATIONSHIP OF THE SOIL FAUNA TO THE DEVELOPMENT OF SOIL TYPES AND TREE NUTRITION IN THE TEMPERATE ZONE

Before discussing the role of animals in the formation of soil types, the two soils dealt with must be described and such terms as are subject to diverse usage must be defined for the purposes of this paper. The use of 'humus' follows Waksman (1938) who defines it as 'all the plant and animal residues brought upon or into the soil and undergoing decomposition'. 'Soil' here includes both mineral and organic materials whether these occur in discrete layers or not, whilst 'litter' designates the annual leaf fall as indicated by the layer of apparently uneaten and undecomposed sticks, fruits, leaves, etc. on the surface of the soil.

The two soil types discussed are known as the podsol and the Brown Forest Soil, the first being typically developed under coniferous forest and the latter under deciduous forest. The humus accumulation in the podsol is variously described as 'mor' or 'duff', whilst in the Brown Forest Soil it is termed 'mull'.

The most marked difference between the two soil types is the distribution of the organic matter. In the podsol the humus forms a distinct layer on the surface of the mineral soil; whilst in the Brown Forest Soil the annual leaf fall is rapidly removed from the surface horizon and the humus is found intimately mixed with the mineral matter of the upper 8 in. or so of soil, giving it a characteristic dark brown appearance. The corresponding upper layer of the podsol is leached to a paler colour than the underlying subsoil. Immediately below the leached layer is a zone of deposition characteristically stained a dark brown. In the Brown Forest Soil this marked zone of deposition is absent, the upper darker layer grading into the

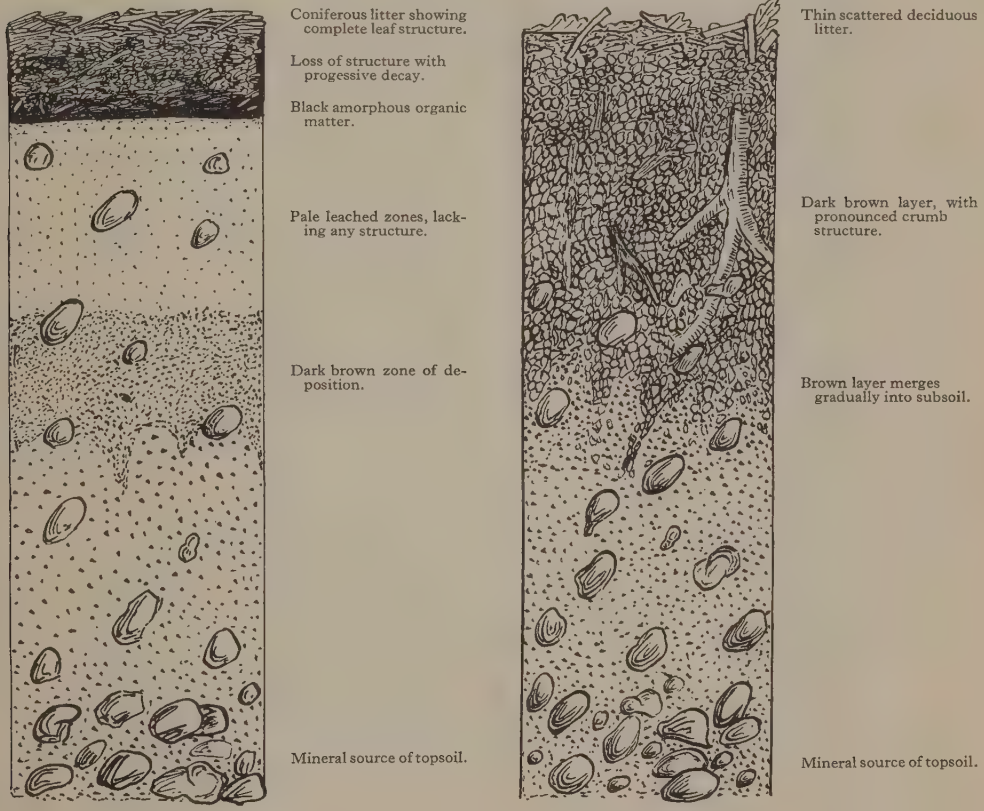
Coniferous litter showing complete leaf structure.
Loss of structure with progessive decay.
Black amorphous organic matter.
Pale leached zones, lacking any structure.
Dark brown zone of deposition.
Mineral source of topsoil.
Podsol
Thin scattered deciduous litter.
Dark brown layer, with pronounced crumb structure.
Brown layer merges gradually into subsoil.
Mineral source of topsoil.
Brown forest soil

Fig. 1. Distribution of humus in coniferous and deciduous forests.

subsoil beneath. The discrete layer of coniferous humus is typically acid in reaction, a condition generally considered responsible for the leaching of the soil beneath. This is in marked contrast to the neutral conditions prevailing in the Brown Forest Soils. These two soil types are diagrammatically represented in Fig. 1, whilst the difference in general surface conditions can readily be seen from Pls. 2, 3.

Jacot (1939) coined the word *endophagous* to describe those animals which as nymphs or adults feed within conifer needles, and *ectophagous* to describe those which consume the leaves in their entirety and from without. This division of the primary saprophagous animals of the soil corresponds to an obvious division in size, the endophagous animals being extremely small whilst the ectophagous animals are relatively large. Using this nomenclature to embrace the soil fauna of both deciduous and coniferous forests we can classify the animals into groups according to their function in the soil as follows:

A. *Ectophagous animals*

(1) Species concerned only with the mechanical subdivision and partial chemical breakdown of the litter.

(*a*) Green leaf eaters, e.g. gastropods, caterpillars, Chrysomelidae, rodents, deer, birds, etc.

(*b*) Annual leaf fall and detritus eaters, e.g. gastropods, Collembola, Acarina, together with some dipterous, Carabid and Staphylinid larvae.

(2) Species concerned not only with the subdivision and breakdown of the litter but also with its incorporation in the soil.

(*a*) Lumbricillids, Formicoidea, Myriapoda (in the tropics and subtropics Isoptera), rodents (more especially, however, under grassland conditions (Grinnell, 1923)).

B. *Endophagous animals*

(1) Specialized dead leaf miners: Hoplodermid mites, Sciarid larvae.

(2) Less specialized forms responsible for tunnelling out dead roots, etc. so providing channels down which the more finely divided decomposition products may be swept (Jacot, 1939), e.g. Oribatid and Tyroglyphid mites, Collembola, dipterous larvae.

C. '*Chemical agents*'

Forms concerned primarily in the chemical conversion of the humus such as bacteria and fungi.

D. *Predators*

(*a*) Those which by reason of their small size make little contribution to the mixture of mineral and organic matter, e.g. Chilopoda, Staphylinidae, Carabidae, Araneae.

(*b*) Those which by reason of their bulk and active fossorial habits make a considerable contribution to the mixing of the mineral and organic fractions of the soil, e.g. moles and more locally rodents and shrews.

E. '*Secondary product eaters*'

Here we may group together the heterogeneous though valuable collection of animals responsible for consuming faeces, fungi and partially decomposed plant material; this group contains the Scarabaeidae, Acarina, Collembola, Nematoda, Enchytraeidae and some species of Lumbricoidea.

F. '*Shelterers*'

Lastly we have those animals which use the soil as a protective cover in which to pass a defenceless resting stage or hibernate. Among this latter group must be included the large assemblage of animals which migrate into the woodland soils at the onset of winter from the tree-tops, pastures, etc. (Blake (1926), Weese (1924)). The major contribution these animals make to the soil is the mixing of its organic and mineral constituents and its enhanced aeration due to their burrowing activities. The chief groups here are larval Lepidoptera, Diptera and Coleoptera, together with adult beetles.

This classification illustrates the variety of functions carried out by the soil fauna, whilst the necessity of using orders and families rather than genera and species is indicative of the paucity of detailed knowledge in this field. In no case could the species of a particular soil be classified according to their feeding habits and effects on the soil, which clearly indicates the need for experimental work to determine the life-history, feeding habits and digestive physiology of the individual species. The only records so far seen of the feeding habits of soil invertebrates are those of Darwin (1881), and Johnson, quoted by Gast (1937), on the food preferences of the earthworm *Lumbricus terrestris*, Jacot's work (1939) on mite nymphs feeding within coniferous needles and Romell's (1935) observations on the millipedes *Fontaria trimaculata* and *coriacea*.

Perhaps the best illustration we have of the habits of the various species of a single order is provided by the Lumbricidae. Table 1, drawn from Bornebusch's work (1930), illustrates the different habits of a few species of earthworm and again emphasizes the need for further work on other orders. Romell (1935) has accorded the millipedes *F. trimaculata* and *coriacea* a role similar to that of earthworms, in the formation of mull under a white pine canopy in the Adirondacks. An interesting point observed in pot experiments was that the millipedes only ate leaves previously attacked by fungi. In this case the mixing of the organic and mineral materials was achieved by the animal eating the soil as well as the litter.

Photo. 1. Douglas fir plot, Bagley Wood, Oxford. Clean floor typical of coniferous woodland under which podsol soil conditions tend to develop.

Photo. 2. Rather open oak woodland in June, Bagley Wood, Oxford. Heavy growth of herbaceous plants typical of deciduous woodland associated with brown forest soils. Canopy of oak with ground flora dominated by *Pteridium aquilinum* and *Scilla non-scripta*.

Humus. Besides the humus exerting a profound effect on the structure, water retaining capacity and fertility of the soil, it acts as the major reservoir of carbon dioxide, nitrogen and other inorganic substances such as phosphorus, potassium, sodium, calcium, magnesium and iron, to say nothing of the rarer elements such as boron, manganese, nickel, etc.

The conspicuous layer of humus on the surface of podsols was at one time thought to represent a much larger concentration of humus, due to slower decomposition, than that found in the Brown Forest Soils. This idea has been challenged by that of Romell (1935*b*) who showed that the rate of decomposition within, and organic content of, the top 30 cm. of both soils was approximately the same. He further confirmed the work of Hesselman (1926), showing that in podsols the nitrogen breakdown was generally terminated by the production of ammonia compounds whilst in the Brown Forest Soils nitrates represented the corresponding end-products. Romell's arguments left, however, one point undiscussed, namely the so-called fertility of the Brown Forest Soils. Considering that the rate of decomposition and production of nitrogen was approximately equal in both soils, a difference of fertility seems an anomaly. It is here suggested that the discrepancy is introduced by the definition of fertility. Fertility as generally understood is the capacity of a site to produce agricultural crops, for which the site after a hardwood rotation is definitely more preferable. Considering, however, that the volume of coniferous timber produced on many sites is at least equal to that of the deciduous timber which could be produced on the same site, it would appear better to estimate fertility in terms of the plant material produced per acre. Using this conception the anomaly is resolved.

In the podsol the organic matter accumulates in a definite layer, in the Brown Forest Soil it is dispersed throughout a large volume of soil. There is ample evidence to show that the chemical decomposition of the organic matter in the podsol is carried out predominantly by fungi whilst in the Brown Forest Soil the larger part of the decomposition is due to bacteria (Waksman, Tenney & Stevens, 1928; Cobb, 1932). This difference in the nature of the organisms responsible for the decomposition of the plant remains is paralleled by the distribution of the humus, which accumulates in a definite layer in the podsol, whereas in the Brown Forest Soil it is dispersed throughout the upper 8 in. or so of soil. Mineral soil in close contact with humus, particularly under well aerated conditions, is generally considered to favour bacterial action (Gast, 1937).

Table 1. *Bornebusch's data* (1930) *on the distribution of earthworms in Danish forest soils arranged in tabular form to show distribution according to soil type*

	Brown Forest Soils			Podsol type soils		
				Mor		
	Deep mull	Surface mull				
Species	Oak-*Mercurialis*	Beech-*Oxalis*	Spruce-*Oxalis*	Beech-raw humus	Spruce-raw humus	Functional groupings of earthworms
Lumbricus terrestris	×	.	.	.	.	Species penetrating deep into the subsoil. Very efficient mixers of soil and litter
L. rubellus	×	×	×	.	.	
Allolobophora longa	×	.	.	.	.	
Octolasium cyaneum	×	.	.	.	.	
Allolobophora turgida	×	×	.	.	.	Species penetrating surface of mineral soil only. Some mixture of mineral soil takes place
A. trapezoides	×	—	.	.	.	
A. chlorotica	×	—	.	.	.	
Eisenia rosea	×	×	.	.	.	
Lumbricus castaneus	.	×	—	—	—	Species living in litter only. No admixture of litter and mineral soil takes place
Dendrobaena arborea	.	×	—	—	—	
D. octohedra	.	×	×	×	×	

The mixing of the humus and mineral soil is achieved by the larger forms of the mesofauna, the presence of which is normally correlated with that of deciduous trees. It is at this point that it is wished to push the analysis one stage further. The work of Lyford (1943) has shown that the palatability of hardwood leaves to millipedes is closely paralleled by the ash content, and more particularly the calcium content, of the leaves. Similar work by Johnson, quoted by Gast (1937), on the earthworm, *Lumbricus terrestris*, has also shown a correlation between the palatability of various hardwood leaves with their calcium content. Arguing from the data of Lyford and Johnson, it may be suggested that the larger ectophogous animals prefer something in the litter the abundance of which varies directly with that of calcium in the tissues. Thus we see that the formation or otherwise of mull is a reflection of the utilization by the plant of calcium from the mineral soil.

Mull formation. So far, two theories have been suggested for the formation of mull, the first, that of P. E. Müller, expounded and developed by Bornebusch (1930), and the second that of Jacot (1935*a*). Bornebusch (pp. 87–92) has given a very succinct account of the observations dealing with earthworms from the time of Gilbert White (d. 1789) to that of his own publication in 1930. He concludes: 'The importance of earthworms* [i.e. more particularly *Lumbricus terrestris*, *Allolobophora turgida*, *A. trapezoides*, *A. longa*, *Octolasium cyaneum* and *O. lacteum*] in the formation of soil [Brown Forest Soils and agricultural soils], we can briefly characterize as follows: They convey vegetable matter into the ground, where they devour it after it has turned soft; this accelerates the transmutation of all deciduous products. They riddle through and through the upper mully part of the topsoil, thus keeping it friable and porous. They devour a lot of earth, which in the form of worm casts they deposit upon the surface of the ground; these worm casts consist of humus and mineral earth intermixed, constituting a most excellent soil for plants to grow in. Not merely the upper loose layer of mull, but the entire mully topsoil is presumably due to earthworm excrements, gradually deposited on the surface of the ground; hence the topsoil contains only little coarse mineral matter. Finally, earthworms form intersecting burrows in the subsoil, to which they resort whenever the weather is very dry or very cold, and these passages serve as drains for water and as tracks for roots to layers of soil underneath.'

Earthworms and other mobile animals further facilitate the early decay of organic matter by transporting bacteria and fungi wherever they move in the soil. To this must be added the fact that wherever we find an abundant supply of earthworms, we also find such predators as moles, Lithobiidae, Carabidae and larger Staphylinidae. The mixture of mineral soil with the humus is generally considered to enhance bacterial activity in the soil at the expense of fungal activity, but direct experimental evidence on this point appears to be wanting.

It may be noted that the biomass of worms in a rich oak-*Mercurialis* soil is the same as that of the livestock on a first class Danish farm (Bornebusch, 1930), and that Wolcott (1937) records that in rough pasture the biomass of insects is equal to, and their consumption of grass greater than, that of the stock on the same area. The last figure, although not in itself applicable to forest conditions, does at least give some idea of the probable insect population at work in a deciduous woodland where both the canopy and herbaceous ground flora carry a high population of insects, etc. The rain of faeces under such a condition forms an important contribution to the litter and Stoklasa (1929) has suggested that the caterpillars feeding in the canopy are an active agent in the distribution of the cellulose decomposing bacteria. Green, and in particular, young leaves, have a higher ash content than the autumn fall and it may be that the much higher insect population in an oak wood by supplying calcium-rich faeces to the litter contribute significantly to the ready decomposition of the humus in such woodland.

Jacot (1935, etc.) maintains that one of the prime factors in mull formation is the development of a dense ground flora of herbaceous annuals. With such plants there is an extensive annual crop of rootlets for the soil animals, and in particular the Oribatid mites, to eat out. Jacot further remarks that not only do these dead root eaters hollow out the rootlets, but they leave in the channel a thin thread of their faeces, the faeces subsequently being washed out and distributed throughout the soil. Although it is true to say that a herbaceous ground flora is typical of Brown Forest Soils and normally absent in podsol soils, I would not weight the role of ground vegetation so high or view it from quite the same standpoint as Jacot. Whilst not denying that humus is mixed with the mineral soil in the manner suggested, it is also true to say that herbaceous vegetation provides food for worms and so contributes to the formation of mull by maintaining a high population of these creatures. Only laboratory experiments, however, can indicate the relative importance of these 'mechanisms' in the formation of mull soils.

Podsol formation. The formation of a podsol profile with a mor topsoil is for the greater part associated with a coniferous canopy where the larger ectophagous animals are absent, due possibly to a low calcium content in the litter or the highly distasteful resinous layer of the leaves (Nemec). The fauna here consists of a large number of small animals as contrasted with that of the Brown Forest Soil which consists of larger animals in relatively small numbers. Jacot (1939) records three species of mite, *Hoplophorella thoreaui*, *Phthiracarus boresetosus* and *Adoristes ovatus* as having nymphal stages which feed and develop on the mesophyll of conifer needles. Also he records a Sciarid fly larva *Phaenocladius* which feeds similarly or more probably on the faeces of the mite nymphs.

Further relationships of animals to humus decomposition. The activities of the animals, however, are not restricted to the mechanical subdivision of the humus but they also play a part in its chemical transformation. Bornebusch's (1930) calculations of the respiration of the soil fauna show that it constitutes a considerable part of the carbon-dioxide evolution of forest soils. Further, the animals excrete their waste nitrogen as relatively simple nitrogenous products such as uric acid (Wigglesworth, 1939), thus accelerating the return of nitrogen to the plants.

* Species list within brackets inserted by author.

The animals, in addition to breaking up the humus mechanically and chemically in the process of feeding and digestion, pass faeces which by virtue of the small size of the organic particles present an enormously larger surface to the attack of bacteria and fungi, thus materially speeding up the rate of decay.

A further contribution of animals to the decay of the litter may perhaps be surmised from the work of Rayner (Rayner & Neilson-Jones, 1944) on composts. The improved nature of composts using an animal source of nitrogen such as dried blood as distinct from an inorganic source as suggested by Rayner, would indicate the possibility of the accumulation of animal bodies within the soil providing a factor of some importance in determining the course of decomposition of the litter and its conversion to a satisfactory medium for plant nutrition. If this suggestion is correct, we may expect a higher degree of fertility with an increasing animal mass within the soil not merely because of the direct effects of the animals in maintaining aeration and bringing about decomposition, but because of the effects of the animal proteins, etc. on the course of the decomposition. If decomposition is to proceed rapidly to completion, then the order and identity of the fungi carrying out the decomposition of the substance is of considerable importance. Thus mushroom manure attacked first by cellulose-decomposing fungi and bacteria results in a highly resistant residue unattacked by *Psalliota*, whereas mushroom manure first attacked by a lignin-destroying fungus such as *Psalliota* leaves a residue readily decomposed by the cellulose destroying microflora (Waksman & Allen, 1932; Waksman & Tenney, 1927). Similarly, litter first decomposed by *Coniophera cerebella* is inimicable to the development of *Clitocybe nebularis* (Rayner, 1945).

Assimilation of nitrogen by the plant. To complete the picture of the circulation of carbon and nitrogen, etc. in nature we must consider how the products of decay are rendered available to the plant. The evolution of CO_2 by the respiration of the animal and plant life within the soil and its subsequent reconversion to carbohydrates by photosynthesis is a too well-known story to require more than passing mention here because of its extreme importance. For the rest, we shall confine ourselves to the discussion of the assimilation of such inorganic elements as nitrogen.

Normally beneath a coniferous canopy we find acid soils of the podsol type in which very little, if any, free nitrate is found. The bulk of the humus of such soils accumulates in a well-defined compact layer possessed of a microflora largely consisting of fungi. Such a microflora competes directly with the roots of the trees for water and for mineral salts including the inorganic sources of nitrogen such as nitrates and ammonium salts (Rayner, 1945). The healthy growth of conifers in such soils is associated with the development of vigorous ectotrophic mycorrhiza. The precise nature of the contribution of such mycorrhiza to the health of the tree, whether growth-promoting substances, essential mineral substances or both, remains as yet a subject of controversy, but of their necessity for the healthy growth of the tree there remains no doubt. The enhanced growth of the fungus due to a source of readily assimilable carbohydrate in the roots (Frank, cited by Melin, 1925; Rayner, 1945) or to the excretion of such growth-promoting substances as phosphatides (Melin, 1925) enables the mycorrhizal-forming fungus to compete on particularly favourable terms with the other elements of the microflora for the nitrogen and other substances essential for growth, a proportion of the nitrogen so absorbed being later passed on to a tree. The chief difficulty in the acceptance of this view is the lack of knowledge of the precise means of transference of the nitrogen from the fungus to the tree. Under a deciduous canopy, however, we generally find Brown Forest Soils of a decidedly less acid character than the podsols and characterized by the vigorous production of nitrates (Hesselman, 1926). The trees typically associated with such conditions, e.g. oak and ash, possess a fibrous root system and lack ectotrophic mycorrhiza, though they are often associated with endotrophic mycorrhiza. Here the nitrate is absorbed directly by the fibrous root systems of the trees.

The general system of relationships and circulation of materials in forest soil is summarized tentatively in the diagram in Fig. 2.

4. SUMMARY

1. The soil fauna is briefly reviewed and divided into three size classes here called the micro-, meso-, and macrofauna. The methods used in sampling the whole soil fauna range are outlined.

2. The methods applicable to the mesofauna are discussed in detail and subdivided into the following categories: (1) Direct sorting, (2) Sieving, (3) Flotation, (4) Automatic, (5) Centrifuging and (6) Wetting methods.

3. As these methods sample the different elements of the fauna with varying degrees of accuracy it is necessary to employ several methods in order to obtain a complete picture of the fauna of any one site.

4. The soil animals are grouped, according to their food habits and effects on the soil, under the following heads: (A) Ectophagous animals, (B) Endophagous animals, (C) 'Chemical agents', (D) Predators, (E) 'Secondary Product Eaters', (F) 'Shelterers'. The paucity of detailed information in this field is commented on and the Lumbricidae quoted as the only group about whose ecology even a beginning in this direction has been made.

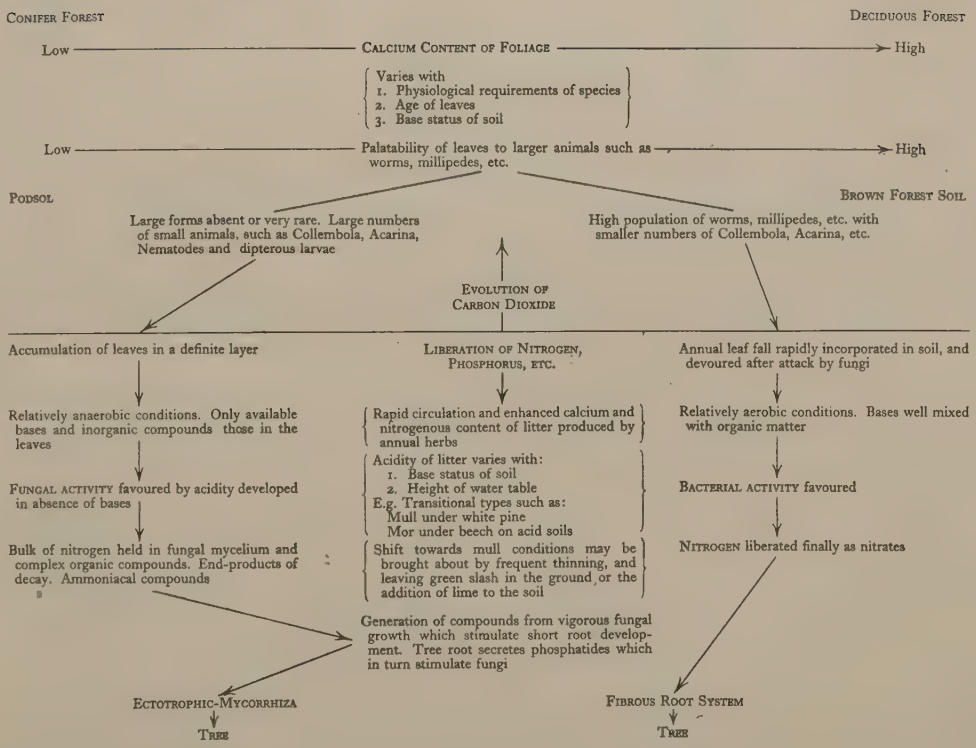
Conifer Forest
Deciduous Forest
Low
Calcium Content of Foliage
High
Varies with
1. Physiological requirements of species
2. Age of leaves
3. Base status of soil
Low
Palatability of leaves to larger animals such as worms, millipedes, etc.
High
Podsol
Brown Forest Soil
Large forms absent or very rare. Large numbers of small animals, such as Collembola, Acarina, Nematodes and dipterous larvae
High population of worms, millipedes, etc. with smaller numbers of Collembola, Acarina, etc.
Evolution of Carbon Dioxide
Accumulation of leaves in a definite layer
Liberation of Nitrogen, Phosphorus, etc.
Annual leaf fall rapidly incorporated in soil, and devoured after attack by fungi
Relatively anaerobic conditions. Only available bases and inorganic compounds those in the leaves
Rapid circulation and enhanced calcium and nitrogenous content of litter produced by annual herbs
Relatively aerobic conditions. Bases well mixed with organic matter
Fungal activity favoured by acidity developed in absence of bases
Acidity of litter varies with:
1. Base status of soil
2. Height of water table
E.g. Transitional types such as:
Mull under white pine
Mor under beech on acid soils
Bacterial activity favoured
Bulk of nitrogen held in fungal mycelium and complex organic compounds. End-products of decay. Ammoniacal compounds
Shift towards mull conditions may be brought about by frequent thinning, and leaving green slash in the ground or the addition of lime to the soil
Nitrogen liberated finally as nitrates
Generation of compounds from vigorous fungal growth which stimulate short root development. Tree root secretes phosphatides which in turn stimulate fungi
Ectotrophic-Mycorrhiza
Tree
Fibrous Root System
Tree

Fig. 2. General relationships and circulation of materials in forest soil.

5. The importance of humus as a reservoir of plant food, the distribution of humus in the soil and the role of the mesofauna in effecting this distribution are described. It is suggested that one of the primary factors determining the distribution of the mesofauna is the palatability of the leaves, which is closely related to their calcium content.

6. The factors at play in the formation of mull are described and particular mention is made of the work and suggestions of Müller, Bornebusch and Jacot in this field.

7. Podsol formation is similarly treated, though here the only experimental work cited is that of Jacot.

8. The part played by animals in the nitrogen cycle and of their action in speeding up and possibly determining the course of decay is outlined.

9. The assimilation of nitrogen by the plant is very briefly touched upon with particular reference to the mycorrhizal habit of trees.

10. An extensive bibliography of publications dealing with the soil fauna and related ecosystem is appended.

SELECTED BIBLIOGRAPHY

Some abstracts are referred to in square brackets *at the end* of references.

Adams, C. C. (1915). 'An ecological study of prairie and forest invertebrates.' Bull. Ill. Lab. Nat. Hist. 2: 33–280.

Allee, W. C. (1926). 'Distribution of animals in a tropical rain-forest with relation to environmental factors.' Ecology, 7: 445–68.

Alway, F. J., Kittredge, J. & Methley, W. J. (1933). 'Composition of the forest floor layers under different forest types on the same soil type.' Soil Sci. 36: 387–98.

Banks, N. (1904). 'A treatise on the Acarina or mites.' Proc. U.S. Nat. Mus. 28: 1–114.

Banner, J. C. (1900). 'Ants as geological agents in the tropics.' J. Geol. 8: 151–3.

Barnes, H. F. (1933). 'Gall midges (Cecidomyidae) as enemies of mites.' Bull. Ent. Res. 24: 215–28.

Barnes, H. F. (1941). 'Sampling for leatherjackets with orthodichlorobenzene emulsion.' Ann. Appl. Biol. 28: 23–8.

Barnes, H. F. & Weil, J. W. (1942). 'Baiting slugs using metaldehyde mixed with various substances.' Ann. Appl. Biol. 29: 56–68.

Baskina, V. & Friedmann, G. (1927). ['A statistical investigation of the animal components of two associations in the Kama flood-plain.'] Trans. Biol. Sci. Res. Inst. Perm. St. Univ. 1: 183–295.

Bates, C. G. & Zon, R. (1922). 'Research methods in the study of forest environment.' Bull. U.S. Dep. Agric. 1059: 1–209.

Baweja, K. D. (1937). 'The calculation of soil population figures.' J. Anim. Ecol. 6: 366–7.

Baweja, K. D. (1939). 'Studies of the soil fauna with special reference to the recolonization of sterilized soil.' J. Anim. Ecol. 8: 120–61.

Beddard, F. E. (1895). 'A monograph of the order of Oligochaeta.' Oxford.

Beebe, C. W. (1916). 'Fauna of four square feet of jungle debris.' Zoologica, N.Y. 2: 107–19.

Bei-Bienko, G. Ya., Grigor'eva, T. G. & Chetuirkina, I. A. (1936). ['Character of the surface and soil fauna in the Steppe biocenoses near Saverovka village, Orenburg province.'] Summ. Sci. Res. Work, Inst. Pl. Prot. Leningr. for 1935, 78–82. [1937, Rev. Appl. Ent. A, 25: 141.]

Berezina, V. M. (1937). 'Die Veränderung der Entomofauna des Bodens beim Uebergang aus Steppenverhältnissen in Waldverhältnisse.' Rev. Ent. U.R.S.S. 27: 77–112.

Berezina, V. M. (1940). ['Effect of hydrothermal soil conditions on the vertical migration of the cockchafer larvae *Melolontha hippocastani*.'] Bull. Pl. Prot., Leningr. 5: 43–56. [1942, Rev. Appl. Ent. A, 30: 332–3.]

Berlese, A. (1905). 'Apparecchio per raccogliere presto ed in gran numero piccoli Artropod.' Redia, 2: 85–9.

Berwick, E. J. H. (1934–5). 'A preliminary survey of the soil fauna of some Trinidad agricultural lands.' Unpubl. dissertation. Imp. Coll. Trop. Agric. Libr., Trinidad.

Bird, H. (1921). 'Soil acidity in relation to insects and plants.' Ecology, 2: 193–7.

Blair, I. D. (1943). 'Behaviour of the fungus *Rhizoctonia solani* Kühn in the soil.' Ann. Appl. Biol. 30: 118–27.

Blake, I. H. (1926). 'A comparison of the animal communities of conifers and deciduous forests.' Ill. Biol. Monogr. 10: 371–512.

Blake, I. H. (1931). 'Further studies on deciduous forest animal communities.' Ecology, 12: 508–27.

Boitzova, M. K. (1931). ['The animal population of lower layers of the *Pinetum cladinosum*.'] Sci. Rep. Perm. St. Univ. 4: 97–152.

Bornebusch, C. H. (1930). 'The fauna of the forest soil. Skovbundens dyreverden.' Forstl. Forsøgsv. Dan. 11: 1–224.

Bornebusch, C. H. (1940). 'Skovbundens dyreliv.' Tidsskr. Skogbr. 48: 293–309. [1941, Biol. Abstr. 15: 7087, entry.]

Bornebusch, C. H. & Heiberg, S. O. (1936). 'Proposal to the Third International Congress of Soil Science, Oxford, England, 1935, for the nomenclature of forest humus layers.' Trans. Third Int. Congr. Soil Sci. 3: 260–1.

Bouyoucos, G. J. (1913). 'An investigation of soil temperature and some of the most important factors influencing it.' Tech. Bull. Mich. Agric. Exp. Sta. 17: 1–196. [1914, Exp. Sta. Rec. 29 (1913): 618–20.]

Bouyoucos, G. J. (1916). 'Soil temperature.' Tech. Bull. Mich. Agric. Exp. Sta. 26: 1–133. [1917, Exp. Sta. Rec. 35 (1916): 620–2.]

Brian, P. W. & Hemming, H. G. (1945). 'Gliotoxin, a fungistatic metabolic product of *Trichoderma viride*.' Ann. Appl. Biol. 32: 214–20.

Brian, P. W., Hemming, H. G. & McGowan, J. C. (1945). 'Origin of toxicity to mycorrhiza in Wareham Heath soil.' Nature, Lond. 155: 637–8.

Brodskii, A. L. (1928). ['Contributions to the knowledge of the Turkestan soil fauna.'] Proc. 3rd Russ. Congr. Zool. Anat. Hist. 3: 67–8.

Brown, M. J. (1931). 'Comparative studies of the animal communities of oak-hickory forests in Missouri and Oklahoma.' Publ. Univ. Okla. Biol. Surv. 3: 231–61.

Bruce, W. G. (1939). 'Some observations on insect edaphology.' J. Kans. Ent. Soc. 12: 91–3.

Bryantzev, B. (1926). ['On a method for studying the composition of soil entomofauna.'] Zashch. Rast. Vredit. [Bull. Pl. Prot., Leningr.] 3: 420–1.

Bryson, H. R. (1931). 'The interchange of soil and subsoil by burrowing insects.' J. Kans. Ent. Soc. 4: 17–24.

Bryson, H. R. (1933). 'The amount of soil brought by insects to the surface of a watered and an unwatered plot.' J. Kans. Ent. Soc. 6: 81–90.

Bryson, H. R. (1939). 'The identification of soil insects by their burrow characteristics.' Trans. Kans. Acad. Sci. 42: 245–54.

Buckle, P. (1921*a*). 'A preliminary survey of the soil fauna of agricultural land.' Ann. Appl. Biol. 8: 135–45.

Buckle, P. (1921*b*). 'On the ecology of soil insects on agricultural land.' J. Ecol. 11: 93–102.

Bukovskii, V. (1936). ['Die Tierbevölkerung der Wirbellosen des Krimschen Buchenwaldes.'] Trans. State Reservations, 2: 5–103.

Bünzli, G. H. (1935). 'Untersuchungen über coccidophile Ameisen aus den Kaffeefeldern Surinam.' Mitt. Schweiz. Ent. Ges. 16: 453–593.

Burger, H. (1922). 'Physikalische Eigenschaften der Wald- und Frielandböden.' Mitt. Schweiz. ZentAnst. Forstl. Versuchsw. 13: 1–221.

Cambridge, O. Pickard- (1890). 'On the British species of Phalangidea or harvestmen.' Proc. Dorset Nat. Hist. Fld Cl. 11: 163–216.

Cambridge, O. Pickard- (1892). 'On the British species of false-scorpions. Pseudo-Scorpiones—Cambr. & Thorell. Chernetes—Sim.' Proc. Dorset Nat. Hist. Fld Cl. 13: 199–231.

Cameron, A. E. (1913). 'General survey of the insect fauna of the soil within a limited area near Manchester....' J. Econ. Biol. 8: 159–204.

Cameron, A. E. (1917). 'The insect association of a local environmental complex in the district of Holmes Chapel, Cheshire.' Trans. Roy. Soc. Edinb. 52: 37–78.

Cameron, A. E. (1925). 'Soil insects.' Sci. Progr. Twent. Cent. 20: 92–108.

Campbell, R. E. (1937). 'Temperature and moisture preferences of wireworms.' Ecology, 18: 479–89.

Carpenter, J. R. (1936). 'Quantitative community studies of land animals.' J. Anim. Ecol. 5: 231–45.

Carpenter, J. R. & Ford, J. (1936). 'The use of sweep net samples in an ecological survey.' J. Soc. Brit. Ent. 1: 155–61.

Carter, W. (1925). 'The effect of low temperatures on *Bruchus obtectus* Say, an insect affecting seed.' J. Agric. Res. 31: 165–82.

Chapman, R. N. (1931). 'Animal ecology with especial reference to insects.' New York.

Chapman, A. J. & Cavitt, H. S. (1934). 'The influence of soil moisture upon survival of the pink bollworm.' J. Econ. Ent. 27: 820–7.

Chapman, R. N., Mickel, C. E., Parker, J. R., Miller, G. E. & Kelly, E. G. (1926). 'Studies in the ecology of sand dune insects.' Ecology, 7: 416–26.

Chetuirkina, I. (1928). ['Distribution of the Lumbricidae in the soils of the Troitsk District, Ural Region.'] Trav. Inst. Rech. Biol. Perm. 2: 433–68.

Cobb, M. J. (1932). 'A quantitative study of the micro-organic population of a hemlock and deciduous forest soil.' Soil Sci. 33: 325–45.

Cobb, N. A. (1915). 'Nematodes and their relationships.' Yearb. U.S. Dep. Agric. 1914: 457–90.

Cobb, N. A. (1918). 'Estimating the nematode population of the soil.' Tech. Circ. U.S. Dep. Agric. No. 1: 1–48.

Connell, A. B. (1923). 'Measuring soil temperature by standard thermometer suspended in iron pipe.' Ecology, 4: 313–16.

Cook, W. C. (1924). 'Climatic variations and moth flight at Bozeman.' Canad. Ent. 56: 229–34.

Cook, W. C. (1927). 'Studies in the ecology of Montana cutworms (Phalaenidae)....' Ecology, 8: 156–73.

Cook, W. C. (1928). 'Light traps as indicators of cutworm moth population.' Canad. Ent. 60: 103–9.

Corbet, A. S. (1935). 'Biological processes in tropical soils with special reference to Malaysia.' Cambridge.

Criddle, N. (1918). 'The habits and control of white grubs in Manitoba.' Agric. Gaz. Can. 5: 449–54.

Cutler, D. W. (1920). 'A method for estimating the number of active Protozoa in the soil.' J. Agric. Sci. 10: 135–43.

Cutler, D. W. & Crump, L. M. (1920). 'Daily periodicity in the numbers of active soil flagellates: with a brief note on the relations of trophic amoebae and bacterial numbers.' Ann. Appl. Biol. 7: 11–24.

Cutler, D. W. & Crump, L. M. (1935). 'Problems in soil microbiology.' London.

Dammerman, K. W. (1925). 'First contribution to a study of the tropical soil and surface fauna.' Treubia, 6: 107–39.

Dammerman, K. W. (1936). 'Enkele gegevens over de tropische bodenfauna.' Trop. Natuur.: 127–32.

Dammerman, K. W. (1937). 'Second contribution to a study of the tropical soil and surface fauna.' Treubia, 16: 121–47.

Daniels, L. B. (1933). 'A flotation method for determining abundance of potato flea beetle larvae.' J. Econ. Ent. 26: 1175–7.

Darwin, C. (1881). 'The formation of vegetable mould, through the action of worms, with observations on their habits.' London.

Davies, W. M. (1928*a*). 'On the economic status and bionomics of *Smynthurus viridis*, Lubb. (Collembola).' Bull. Ent. Res. 18: 291–6.

Davies, W. M. (1928*b*). 'The effect of variation in relative humidity on certain species of Collembola.' Brit. J. Exp. Biol. 6: 79–86.

Decoppet, M. (1920). 'Le hanneton.' Lausanne.

Diebold, C. H. (1935). 'Some relationships between soil type and forest site quality.' Ecology, 16: 640–7.
Diem, C. (1903). 'Untersuchungen über die Bodenfauna in den Alpen.' St. Gallen.
Dillon, G. F. (1938). 'The biology and ecology of the corn seed beetle, *Agonoderus pallipes* Fab. (Carabidae).' Master's Thesis, Kansas State College Library.
Diver, C. (1938). 'The plant-carpet in relation to animal distribution.' Proc. Linn. Soc. Lond. 150: 124–35.
Donahue, R. L. (1940). 'Forest-site quality studies in the Adirondacks. 1. Tree growth as related to soil morphology.' Mem. Cornell Agric. Exp. Sta. 229: 1–44.
Dowdy, W. W. (1944). 'The influence of temperature on vertical migration of invertebrates inhabiting different soil types.' Ecology, 25: 449–60.
Dubos, R. J. (1928). 'Influence of environmental conditions on the activities of cellulose decomposing organisms in the soil.' Ecology, 9: 12–27.
Eaton, T. H. (1942). 'Earthworms of the northeastern United States, a key with distribution records.' J. Wash. Acad. Sci. 32: 242–9.
Eaton, T. H. & Chandler, R. F. (1942). 'The fauna of forest-humus layers in New York.' Mem. Cornell Agric. Exp. Sta. 247: 26. [1943, For. Abstr. 4: 214.]
Edwards, E. E. (1929). 'A survey of the insect and other invertebrate fauna of permanent and arable land of certain soil types at Aberystwyth.' Ann. Appl. Biol. 16: 299–323.
Elton, C. (1930). 'Animal ecology and evolution.' Oxford.
Falck, R. (1928). 'Zwei natürliche Prozesse der Cellulose- und des Lignin-abbaues der verholzten Membran durch Bakterien.' Cellulose-Chem. 9: 1–6.
Falconer, W. (1910). 'Keys to the families and genera of British spiders, and to the families, genera and species of British harvestmen and pseudoscorpions.' Naturalist: 438–47.
Fidler, J. H. (1936). 'An investigation into the relation between chafer larvae and the physical factors of their soil habitat.' J. Anim. Ecol. 5: 333–47.
Fink, D. E. (1927). 'The application of studies in hydrogen ion concentration to entomological research.' Ann. Ent. Soc. Amer. 20: 503–12.
Finney, D. J. (1941). 'Wireworm populations and their effect on crops.' Ann. Appl. Biol. 28: 282–95.
Fisher, R. T. (1928). 'Soil changes and silviculture on the Harvard Forest.' Ecology, 9: 6–11.
Fleming, W. E. & Baker, F. E. (1936). 'A method for estimating populations of larvae of the Japanese beetle in the field.' J. Agric. Res. 53: 319–31.
Forbes, S. A. (1907). 'On the life-history, habits and economic relations of the white grubs and may beetles.' Bull. Ill. Agric. Exp. Sta. No. 116: 447–80. [1908, Exp. Sta. Rec. 19: 554.]
Forbes, S. A. (1916). 'The influence of trees and crops on injury by white-grubs.' Bull. Ill. Agric. Exp. Sta. 187: 259–65.
Ford, J. (1935). 'The animal population of a meadow near Oxford.' J. Anim. Ecol. 4: 195–207.
Ford, J. (1936). 'A method of counting large samples of small arthropods.' J. Anim. Ecol. 5: 396–7.
Ford, J. (1937). 'Fluctuations in natural populations of Collembola and Acarina.' J. Anim. Ecol. 6: 98–111.
Ford, J. (1938). 'Fluctuations in natural populations of Collembola and Acarina. Part 2.' J. Anim. Ecol. 7: 350–69.
Formozov, A. N. & Voronov, A. G. (1939). ['The activity of rodents on the pasture and meadow lands of West Kazakhstan and its economic importance.'] Sci. Rep. Moscow Sta. Univ. 20: 3–122.
Fourman, K. L. (1939). 'Lebensbedingungen und Verhaltensweisen der Bodenfauna forstlicher Standorte.' Miss. Forstwirt. Forstwiss. 10: 160–8.
Fowells, H. A. & Stephenson, R. E. (1934). 'Effect of burning on forest soils.' Soil Sci. 38: 175–81.
Frenzel, G. (1936). 'Untersuchungen über die Tierwelt des Wiesenbodens.' Jena.
Friederichs, K. (1930). 'Die Grundfragen und Gesetzmässigkeiten der land- und forstwirtschaftlichen Zoologie insbesondere der Entomologie.' Berlin. Vol. 1.
Fröbrich, G. (1939). 'Untersuchungen über Vitaminbedarf und Wachstumsfaktoren bei Insekten.' Z. Vergl. Physiol. 27: 335–83.
Fryer, J. C. F. *et al.* (1942). 'Symposium on wireworm investigations.' Ann. Appl. Biol. 29: 144–96.
Fulton, B. B. (1928). 'Some temperature relations of *Melanotus* (Coleoptera, Elateridae).' J. Econ. Ent. 21: 889–97.
Gast, P. R. (1937). 'Contrasts between the soil profiles developed under pines and hardwoods.' J. For. 35: 11–16.
Gause, G. F. (1937). 'Experimental populations of microscopic organisms.' Ecology, 18: 173–9.
Gause, G. F. & Witt, A. A. (1935). 'Behaviour of mixed populations and the problem of natural selection.' Amer. Nat. 69: 596–609.
Gause, G. F., Smaragdova, N. P. & Witt, A. A. (1936). 'Further studies of interaction between predators and prey.' J. Anim. Ecol. 5: 1–18.
Ghilarov, M. S. (1937). 'The fauna of injurious soil insects of arable land.' Bull. Ent. Res. 28: 633–7.
Gilyarov, M. S. (1939). ['The soil fauna and the life of the soil.'] Pedology, No. 6: 3–15.
Gilyarov, M. S. (1941). ['Methods for taking censuses of the soil fauna.'] Pochvovedenie [Pedology], No. 4: 48–77. (Translation in Bureau of Animal Population, Oxford.)
Glasgow, J. P. (1939). 'A population study of subterranean soil Collembola.' J. Anim. Ecol. 8: 323–53.
Golovyanko, Z. S. (1936). ['Les larves plus communes des Coléoptères Lamellicornes de la partie européenne de l'U.R.S.S.' Tabl. Anal.] Faune U.R.S.S. No. 20: 65 pp.
Graham, S. A. (1925). 'The felled tree trunk as an ecological unit.' Ecology, 6: 397–411.
Grankina, K. (1936). ['Washing of the soil as a method for recording small soil insects.'] Pl. Prot., Leningr. 9: 124–5. [1938, Rev. Appl. Ent. A, 25: 396–7.]
Grigoreva, T. G. (1938). ['On methods of estimating the soil fauna.'] Pl. Prot., Leningr. 17: 97–110.
Grinnell, J. (1923). 'The burrowing rodents of California as agents in soil formation.' J. Mammal. 4: 137–49.
Gustafson, A. F. (1941). 'Soils and soil management.' New York.

Haarløv, N. (1942). 'A morphological—systematic—ecological investigation of Acarina and other representatives of the microfauna of the soil round Mørkefjord, northeast Greenland.' Medd. Grønland, 128, No. 1: 1–71.

Haig, I. T. (1938). 'Forest wildlife and silviculture.' Science, 87: 485–7.

Hammer, M. (1937). 'A quantitative and qualitative investigation of the microfauna communities of the soil at Angmagssalik and in Mikis Fjord.' Medd. Grønland, 108, No. 2: 1–53.

Hammer, M. (1944). 'Studies on the Oribatids and Collemboles of Greenland.' Medd. Grønland, 141, No. 3: 1–210.

Handschin, E. (1929). 'Urinsekten oder Apterygota (Protura, Collembola, Diplura und Thysanura).' Tierwelt Dtsch. Pt. 16: 150 pp.

Harris, G. C. M. (1945). 'Chemical changes in beech litter due to infection by *Marasmius peronatus* (Bolt.) Fr.' Ann. Appl. Biol. 32: 38–9.

Haskell, E. F. (1940). 'Mathematical systematization of "environment", "organism" and "habitat".' Ecology, 21: 1–16.

Hawkins, J. H. (1936). 'The bionomics and control of wireworms in Maine.' Bull. Me. Agric. Exp. Sta. 381: 1–146. [1937, Exp. Sta. Rec. 75 (1936): 817–18.]

Hayes, W. P. & McColloch, J. W. (1928). 'Ecological studies of Kansas Scarabaeid larvae (Coleop.).' J. Econ. Ent. 21: 249–60.

Hensen, V. (1877). 'Die Thätigkeit des Regenwurms (*Lumbricus terrestris* L.) für die Fruchtbarkeit des Erdbodens.' Z. Wiss. Zool. 28: 354–64.

Hesselman, H. (1926). 'Studier över barrskogens humustäcke, des egenskaper och beroende av skogsvården.' Medd. Skogsförsöksanst. 22: 169–552.

Heyward, F. & Tissot, A. N. (1936). 'Some changes in the soil fauna associated with forest fires in the longleaf pine region.' Ecology, 17: 659–66.

Hilgard, E. W. (1914). 'Soils, their formation, properties, composition, and relations to climate and plant growth in the humid and arid regions.' New York.

Hoffmann, R. W. (1931). 'Die Tiere. Leben und Wirken der für den Boden wichtigen Tiere.' In Blanck, E., 'Handbuch der Bodenlehre,' 7: 381–437. Berlin.

Holdhaus, K. (1910). 'Die Siebetechnik zum Aufsammeln der Terricolfauna (nebst Bemerkungen über die Oekologie der im Erdboden lebenden Tierwelt).' Z. Wiss. InsektBiol. 6: 1–4.

Hope, J. G. (1943). 'An investigation of the litter fauna of two types of pine forest.' Bull. Wagner Inst. Sci. Philad. 18: 1–7.

Houser, J. S. (1918). 'Destructive insects affecting Ohio shade and forest trees.' Bull. Ohio Agric. Exp. Sta. 332: 165–487.

Howard, L. O. (1931). 'The insect menace.' London.

Hungate, R. E. (1938). 'Studies on the nutrition of *Zootermopsis*. II. Relative importance of the termite and the Protozoa in wood digestion.' Ecology, 19: 1–25.

Ingram, J. W. (1931). 'Soil animals attacking sugar cane.' J. Econ. Ent. 24: 866–9.

Ionescu, M. A. (1932). 'Contribuţiuni le studiul faunei frunzarului (pătura de frunze moarte) de Fag.' Bucharest.

Isaac, L. A. & Hopkins, H. G. (1937). 'The forest soil of the Douglas fir region, and the changes wrought upon it by logging and slash burning.' Ecology, 18: 264–79.

Ivanov, S. P. (1937). ['Handbook on investigation of the harmful soil entomofauna.'] Kiev.

Ivanov, S. P. *et al.* (1930). ['Census methods for the terrestrial fauna.'] Kiev.

Jacot, A. P. (1932). 'A knockdown "Berlese funnel".' Science, 76: 299–300.

Jacot, A. P. (1935*a*). 'Wild life of the forest carpet.' Science Monthly, 40: 425–30.

Jacot, A. P. (1935*b*). 'Molluscan populations of old growth forests and rewooded fields in the Asheville Basin of North Carolina.' Ecology, 16: 603–5.

Jacot, A. P. (1936*a*). 'Why study the fauna of the litter?' J. For. 34: 581–3.

Jacot, A. P. (1936*b*). 'Quantitative litter sampling.' Ecology, 17: 327–8.

Jacot, A. P. (1936*c*). 'Soil structure and soil biology.' Ecology, 17: 359–79.

Jacot, A. P. (1939). 'Reduction of spruce and fir litter by minute animals.' J. For. 37: 858–60.

Jacot, A. P. (1940). 'The fauna of the soil.' Quart. Rev. Biol. 15: 28–58.

Jary, S. G. (1942). 'Wireworms and crop production.' Ann. Appl. Biol. 29: 150–5.

Jegen, C. (1920). 'Die Bedeutung der Enchytraeiden für die Humusbildung.' Landw. Jb. Schweiz, 34: 55–71.

Joachim, A. W. R. & Kandiah, S. (1940). 'Studies on Ceylon soils. XIV. A comparison of soils from termite mounds and adjacent land.' Trop. Agriculturist, 95: 333–8.

Johnston, J. W. (1940*a*). 'Forest soil biota in relation to soil transformation.' Fox Forest Notes, No. 22.

Johnston, J. W. (1940*b*). 'A mull-forming biota under the red and white pine type.' Fox Forest Notes, No. 23.

Jones, E. W. (1937). 'Practical field methods of sampling soil for wireworms.' J. Agric. Res. 54: 123–34.

Kalshoven, L. G. E. (1941). 'Invloed van de locale macroscopische fauna, en met name van de termieten, op de vruchtbaarheid van den bodem.' ['Influence of the local macroscopic fauna, especially the termites on soil fertility' (with discussions).] Tectona, 34: 568–82.

King, K. M. (1927). 'A quantitative and comparative investigation of the fauna of natural and ruderal associations at Saskatoon, with specific references to climatic influences.' Bull. Ecol. Soc. Amer. 8.

King, K. M. (1929). 'The value of quantitative methods in the investigation of field crop insects, with special reference to work with wireworms and cutworms.' Trans. 4th Int. Congr. Ent. 2: 248–58.

King, K. M. (1928). 'Economic importance of wireworms and false wireworms in Saskatchewan.' Sci. Agric. 8: 693–706.

King, K. M. (1939). 'Population studies of soil insects.' Ecol. Monogr. 9: 270–86.

King, K. M. & Atkinson, N. J. (1927). 'Quantitative methods of collecting and rearing soil cutworms.' J. Econ. Ent. 20: 821–30.

King, K. M. & Atkinson, N. J. (1928). 'The biological control factors of the immature stages of *Euxoa ochrogaster* Gn. (Lepidoptera, Phalaenidae) in Saskatchewan.' Ann. Ent. Soc. Amer. 21: 167–88.

King, K. M. & Glen, R. (1933). 'A co-operative investigation of the quantitative relation between summer-fallow methods and the wireworm in Saskatchewan.' Sci. Agric. 13: 646–52.

King, K. M., Paul, L. C., Glen, R. & Berg, V. L. (1936). 'Summary of Saskatchewan grasshopper infestations autumn 1935 and ratings of probable outbreaks 1936.' Saskatoon Leafl. Ent. Br. Canad. Dep. Agric. 42: 78 pp. [1936, Rev. Appl. Ent. A, 24: 444–5.]

Kotovschikova, M. A. (1936). ['Examination of methods of work employed by rodent census observation posts.'] Summ. Sci. Res. Work, Pl. Prot. Inst. 1935: 540–2. (Translation in the Bureau of Animal Population, Oxford.)

Kratochvil, J. (1936). ['Troisième notice à la connaissance de la faune du sol. Metamorphose de quelques Lyconiides du sol des forêts.'] Bull. Inst. Nat. Agron. Brno, D, 23: 1–46.

Kseneman, M. (1938). ['Beiträge zur Kenntnis der Beziehungen der Apterygoten zu den Eigenschaften ihrer Standorte mit besonderer Berücksichtigung der Waldböden.'] Bull. Inst. Nat. Agron. Brno, D, 26: 1–36.

Kubiëna, W. (1944). 'L'investigation microscopique de l'humus.' Z. Weltforstwirt. 10: 387–410.

Ladell, W. R. S. (1936). 'A new apparatus for separating insects and other arthropods from the soil.' Ann. Appl. Biol. 23: 862–79.

Lane, M. C. & Jones, E. W. (1936). 'Flooding as a means of reducing wireworm infestations.' J. Econ. Ent. 29: 842–50.

Lane, M. C. & Shirck, F. H. (1938). 'A soil sifter for subterranean insect investigations.' J. Econ. Ent. 21: 934–6.

Lang, R. (1931). 'Echte und unechte Krümelung und Gare.' Forstw. Centralbl. 53: 309–24, 351–67, 393–403.

Lindquist, A. W. (1933). 'Amounts of dung buried and soil excavated by certain Coprini (Scarabaeidae).' J. Kans. Ent. Soc. 6: 109–23.

Lindquist, B. (1941*a*). 'Experimentelle Untersuchungen über die Bedeutung einiger Landmollusken für die Zersetzung der Waldstreu.' K. Fysiograf. Sällsk. Lund. Förh. 11: 144–56. [Chem. Abstr. 37: 2502.]

Lindquist, B. (1941*b*). 'Undersökningar över några skandinaviska daggmaskarters betydelse för lövförnans omvandling och för mulljordens struktur i svensk skogsmark.' Svenska SkogsvFören. Tidskr. 39: 179–242.

Lomakina, N. (1936). ['Working out and improving of census methods for mouse-like rodents in forcing beds, ricks and buildings.'] Summ. Sci. Res. Work, Inst. Pl. Prot., Leningr. 1935: 542–5.

Lubbock, J. (1873). 'Monograph of the Collembola and Thysanura.' London.

Lyford, W. H. (1943). 'The palatability of freshly fallen forest tree leaves to millipeds.' Ecology, 24: 252–61.

MacGill, E. I. (1939). 'A gamasid mite (*Typhlodromus thripsii* n.sp.), a predator of *Thrips tabaci* Lind.' Ann. Appl. Biol. 26: 309–17.

MacLagan, D. S. (1932). 'An ecological study of the "lucerne flea" (*Smynthurus viridis*, Linn.) I [II].' Bull. Ent. Res. 23: 101–45, 151–90.

MacLagan, D. S. (1933). 'The ecological significance of soil reaction (*p*H value) in relation to terrestrial animals.' Proc. R. Phys. Soc. Edinb. 22: 107–22.

Macnamara, C. (1919). 'Popular and practical entomology. Remarks on Collembola.' Canad. Ent. 51: 73–80, 241–5, 265–71.

Macnamara, C. (1924). 'The food of Collembola.' Canad. Ent. 56: 99–105.

McAtee, W. L. (1907). 'Census of four square feet.' Science, 26: 447–9.

McClure, H. E. (1935). 'A soil surface sampler.' Ecology, 16: 666–9.

McColloch, J. W. (1926). 'The rôle of insects in soil deterioration.' J. Amer. Soc. Agron. 18: 143–50.

McColloch, J. W. & Hayes, W. P. (1922). 'The reciprocal relation of soil and insects.' Ecology, 3: 288–301.

McColloch, J. W. & Hayes, W. P. (1923). 'Soil temperature and its influence on white grub activities.' Ecology, 4: 29–36.

McColloch, J. W. & Hayes, W. P. (1929). 'Some problems in the control of underground insects.' Trans. 4th Int. Congr. Ent. 2: 306–15.

McColloch, J. W., Hayes, W. P. & Bryson, H. R. (1927). 'Preliminary notes on the depth of hibernation of wireworms (Elateridae, Coleoptera).' J. Econ. Ent. 20: 561–4.

McColloch, J. W., Hayes, W. P. & Bryson, H. R. (1928). 'Hibernation of certain Scarabaeids and their *Tiphia* parasites.' Ecology, 9: 34–42.

McConnell, W. R. (1915*a*). 'A unique type of insect injury.' J. Econ. Ent. 8: 261–7.

McConnell, W. R. (1915*b*). 'Another nodule-destroying beetle.' J. Econ. Ent. 8: 551.

McDougal, W. B. (1922). 'Symbiosis in a deciduous forest.' Bot. Gaz. 73: 200–12. Ibid. (1925). 79: 95–102.

Mail, G. A. (1930). 'Winter soil temperatures and their relation to subterranean insect survival.' J. Agric. Res. 41: 571–92.

Marsh, G. P. (1874). 'The earth as modified by human action.' London, etc.

Melin, E. (1922). 'On the mycorrhizas of *Pinus sylvestris* L. and *Picea abies* Karst. A preliminary note.' J. Ecol. 9: 254–7.

Melin, E. (1925). 'Untersuchungen über die Bedeutung der Baummykorrhiza. Eine ökologische-physiologische Studie.' Jena. (Reviewed in 1926. J. Ecol. 14: 164–7. Translated by P. Stickel (1930), U.S. Dep. Agric., For. Serv., N.E. For. Exp. Sta., Amherst, Mass.)

Melin, E. (1930). 'Biological decomposition of some types of litter from North American forests.' Ecology, 11: 72–101.

Melvin, A. & Bushland, R. C. (1938). 'Effects of acidity, alkalinity and moisture content of the soil on emergence of *Cochliomyia americana* C. & P.' J. Econ. Ent. 31: 611–13.

Michael, A. D. (1901–3). 'British Tyroglyphidae.' London. 2 vols.

Miles, H. W. (1945). 'Wireworms and food production.' Nature, Lond. 155: 136–8.

[Miles, H. W. & Cohen, M.] (1939). 'Investigations on wireworms and their control.' J. Lancs. Agric. Soc. 1939: 58–79.

Morris, H. M. (1920). 'Observations on the insect fauna of permanent pasture in Cheshire.' Ann. Appl. Biol. 7: 141–55.

Morris, H. M. (1922*a*). 'On a method of separating insects and other arthropods from the soil.' Bull. Ent. Res. 13: 197–200.

Morris, H. M. (1922*b*). 'The insect and other invertebrate fauna of arable land at Rothamsted.' Ann. Appl. Biol. 9: 282–305.

Müller, P. E. (1878). 'Studier over Skovjord, som Bodrag til Skovdyrkingens Theori. 1. Om Bøgemuld og Bøgemor paa Sand og Ler.' Tidsskr. Skovbr. 3: 1–124.

Müller, P. E. (1884). 'Studier over Skovjord Theori 2. Om Muld og Mor i Egeskove og paa Heder.' Tidsskr. Skovbr. 7: 1–232.

Müller, P. E. (1887). 'Studien über die naturlichen Humusformen und deren Einwirkung auf Vegetation und Boden.' Berlin.

Müller, P. E. (1924). 'Bidrag til de Jydske Hedesletters Naturhistorie karup hedeslette og beslaegtede Dannelse en pedalogisk undersøgelse.' Biol. Medd., Kbh. 4, No. 2: 1–244.

Murayama, J. (1935). ['On the biology of some Korean Scarabaeidae.'] Dobuts. Zasshi, 47: 195–7. [In Japanese.] [1935, Rev. Appl. Ent. A, 23: 370.]

Nefedov, N. I. (1930). ['The ants of Troitsk Forest—Steppe Reserve and their distribution among different elements of the landscape.'] Bull. Sci. Res. Inst. Perm. St. Univ. 7: 259–91.

Norman, A. G. (1934). 'The biological decomposition of plant materials. Part IX. The aerobic decomposition of hemicelluloses.' Ann. Appl. Biol. 21: 454–75.

Ökland, F. (1930). 'Quantitative Untersuchungen der Landschneckenfauna Norwegens. I.' Z. Morph. Ökol. Tiere, 16: 748–804.

Park, O. (1940). 'Studies in nocturnal ecology. IX. Further analysis of activity of Panama rain forest animals.' Ecology, 21: 122–34.

Park, O. (1941). 'Concerning community symmetry.' Ecology, 22: 164–7.

Park, O., Allee, W. C. & Shelford, V. E. (1939). 'A laboratory introduction to animal ecology and taxonomy....' Chicago.

Park, O. & Keller, J. G. (1932). 'Studies in nocturnal ecology. II. Preliminary analysis of activity rhythm in nocturnal forest insects.' Ecology, 13: 335–46.

Park, O., Lockett, J. A. & Myers, D. J. (1931). 'Studies in nocturnal ecology with special reference to climax forest.' Ecology, 12: 709–27.

Payne, N. M. (1926). 'The effect of environmental temperatures upon insect freezing points.' Ecology, 7: 99–106.

Pearse, A. S. (1943). 'Effects of burning-over and raking-off litter on certain soil animals in the Duke Forest.' Amer. Midl. Nat. 29: 406–24.

Pearse, A. S. (1946). 'Observations on the microfauna of the Duke Forest.' Ecol. Monogr. 16: 127–50.

Phillips, J. (1931). 'The biotic community.' J. Ecol. 19: 1–24.

Phillips, J. F. V. (1931). 'Quantitative methods in the study of numbers of terrestrial animals in biotic communities: a review, with suggestions.' Ecology, 12: 633–49.

Pillai, S. K. (1922). 'Beiträge zur Kenntnis der Fauna der Waldstreu. Kiefernstreu-Untersuchungen.' Z. Angew. Ent. 8: 1–30.

Plice, M. J. (1934). 'Acidity, antacid buffering, and nutrient content of forest litter in relation to humus and soil.' Mem. Cornell Agric. Exp. Sta. 166: 1–32.

Plice, M. J. (1939). 'The bionomics of some forest soils.' Proc. Soil Sci. Soc. Amer. 4: 346–52.

Ramann, E. (1911). 'Regenwürmer und Kleintiere im Deutschen Waldboden.' Int. Mitt. Bodenk. 1: 138–64.

Ramann, E. (1928). 'The evolution and classification of soils.' Cambridge.

Rawlins, W. A. (1934). 'Experimental studies on the wheat wireworm *Agriotes mancus* Say.' J. Econ. Ent. 27: 308–14.

Rayner, M. C. (1945). 'Trees and toadstools....' London.

Rayner, M. C. & Jones, W. Neilson- (1944). 'Problems in tree nutrition....' London.

Rege, R. D. (1927). 'Bio-chemical decomposition of cellulosic materials, with special reference to the action of fungi.' Ann. Appl. Biol. 14: 1–44.

Remy, P. (1932). 'Sur la faune détriicole des forêts.' C.R. Acad. Sci., Paris, 194: 127–9.

Reynoldson, T. B. (1939). 'On the life-history and ecology of *Lumbricillus lineatus* Mull. (Oligochaeta).' Ann. Appl. Biol. 26: 782–99.

Reynoldson, T. B. (1939). 'Enchytraeid worms and the bacteria bed method of sewage treatment.' Ann. Appl. Biol. 26: 138–64.

Roberts, A. W. Rymer (1919–22). 'On the life history of "wireworms" of the genus *Agriotes* Esch., with some notes on that of *Athous haemorrhoidalis*, F.' Ann. Appl. Biol. 6: 116–35; 9: 306–24.

Robinson, W. (1927). 'The thermocouple method of determining temperatures.' Ann. Ent. Soc. Amer. 20: 513–21.

Robinson, W. (1928). 'Determination of the natural undercooling and freezing points in insects.' J. Agric. Res. 37: 749–55.

Roebuck, A. (1924). 'Destruction of wireworms.' J. Minist. Agric. 30: 1047–51.

Romell, L. G. (1922). 'Die Bodenventilation als ökologischer Faktor.' Medd. Skogsförsöksanst. 19: 281–359.

Romell, L. G. (1930). 'Forest soil research in relation to forestry with particular reference to the northeast.' J. For. 28: 841–8.

Romell, L. G. (1932). 'Mull and duff as biotic equilibria.' Soil Sci. 34: 161–88.
Romell, L. G. (1935*a*). 'An example of myriapods as mull formers.' Ecology, 16: 67–71.
Romell, L. G. (1935*b*). 'Ecological problems of the humus layer in the forest.' Mem. Cornell Agric. Exp. Sta. 170: 1–28.
Romell, L. G. (1939). 'The ecological problem of mycotrophy.' Ecology, 20: 163–7.
Romell, L. G. & Heiberg, S. O. (1931). 'Types of humus layer in the forests of northeastern United States.' Ecology, 12: 567–608.
Salt, G. & Hollick, F. S. J. (1944). 'Studies of wireworm populations. I. A census of wireworms in pasture.' Ann. Appl. Biol. 31: 52–64.
Sandon, H. (1927). 'The composition and distribution of the protozoan fauna of the soil.' Edinburgh.
Saunders, E. (1896). 'The Hymenoptera Aculeata of the British Isles.' London.
Schaerffenberg, B. (1939). 'Untersuchungen über die Coleopteren- und Dipteren-Fauna des Weidebodens.' Z. Angew. Ent. 26: 536–44.
Scourfield, D. J. (1940). 'The microscopic life of the "leaf carpet" of woods and forests.' Essex Nat. 26: 231–46.
Sgonina, K. (1937). 'Zum Sammeln von kleinen Bodentieren.' Zool. Anz. 120: 319–20.
Shaler, N. S. (1891). 'The origin and nature of soils.' 12th Ann. Rep. U.S. Geol. Surv. 1: 213–345.
Shchastny, N. (1939). ['The determination of mites and mite eggs in flour.'] Lab. Prakt. (Sammelband), 44: 5. [1941, Chem. Abstr. 35: 6675.]
Shelford, V. E. (1908). 'Life-histories and larval habits of the tiger beetles (Cicindelidae).' J. Linn. Soc. (Zool.) 30: 157–84.
Shelford, V. E. (1912). 'Ecological succession. IV. Vegetation and the control of land animal communities.' Biol. Bull. Woods Hole, 23: 59–99.
Shelford, V. E. (1913). 'The reactions of certain animals to gradients of evaporating power of air. A study in experimental ecology.' Biol. Bull. Woods Hole, 25: 79–120.
Shelford, V. E. (1914). 'An experimental study of the behaviour agreement among the animals of an animal community.' Biol. Bull. Woods Hole, 26: 294–315.
Shelford, V. E. (1918). 'Physiological problems in the life-histories of animals with particular reference to their seasonal appearance.' Amer. Nat. 52: 129–54.
Shelford, V. E. (1935). 'Sere, climax and influent animals with special reference to the transcontinental coniferous forest of North America.' Ecology, 16: 375–402.
Shelford, V. E. (1937). 'Animal communities in temperate America....' Chicago. 2nd ed.
Shibata, K. (1932). ['Ecology of subterranean insects. 1. Studies on the physical factors affecting the vitality of subterranean insects.'] Trans. Nat. Hist. Soc. Formosa, 22: 50–65.
Shiperovitch, B. (1937). ['Soil fauna in different types of forest.'] Zool. Zh. 16: 301–10.
Shirck, F. H. (1930). 'A soil-washing device for use in wireworm investigations.' J. Econ. Ent. 23: 991–4.
Shnitnikov, V. N. (1928). ['Some results of research on the ecology of small mammals in Leningrad.'] Proc. 3rd Russ. Congr. Zool. Anat. Hist.: 95–6.
Singh, B. N. (1941). 'Selectivity in bacterial food by soil amoebae in pure mixed culture and in sterilized soil.' Ann. Appl. Biol. 28: 52–64.
Skinner, C. E. & Dravis, F. (1937). 'A quantitative determination of chitin destroying microorganisms in soil.' Ecology, 18: 391–7.
Skinner, C. E. & Mellem, E. M. (1944). 'Further experiments to determine the organisms responsible for decomposition of cellulose in soils.' Ecology, 25: 360–5.
Smart, J. (1942). 'Bibliography of key works for the identification of the British flora and fauna.' Publ. Ass. Study Syst. 1: 1–105.
Smirnov, A. M. (1938). ['The antiformin method for the detection of mites in flour and breadstuffs.'] Voprosy Pitaniya, 7: 222–3. [1941, Chem. Abstr. 35: 4106.]
Smith, F. (1928). 'An account of changes in the earthworm fauna of Illinois, and a description of one new species.' Bull. Ill. Nat. Hist. Surv. 17: 347–62.
Smith, C. C. (1940). 'Biotic and physiographic succession on abandoned, eroded farmland.' Ecol. Monogr. 10: 421–84.
Smith, V. G. (1928). 'Animal communities of a deciduous forest succession.' Ecology, 9: 479–500.
Solomon, M. E. (1945). 'Tyroglyphid mites in stored products. Methods for the study of population density.' Ann. Appl. Biol. 32: 71–5.
Spencer, H. & Stracener, C. L. (1930). 'Recent experiments with soil animals attacking roots of sugarcane.' J. Econ. Ent. 23: 680–4.
Stark, V. N. (1926). ['The influence of soil on the injurious insect fauna of poplar.'] Pl. Prot., Leningr. 3: 15–22. [1926, Rev. Appl. Ent. A, 14: 419.]
Stark, V. N. (1930). ['Methods of investigation of the insect fauna of forest soils. 1. The importance of the soil strata.'] Pl. Prot., Leningr. 6: 763–72. [1931, Rev. Appl. Ent. A, 19: 46–7.]
Stark, V. N. (1931). ['The insect fauna of different forest types.'] Pl. Prot., Leningr. 7: 339–43. [1932, Rev. Appl. Ent. A, 20: 232–3.]
Steiner, G. & Heinly, H. (1922). 'The possibility of control of *Heterodera radicicola* and other plant-injurious nemes by means of predatory nemes, especially by *Mononchis papillatus* Bastian.' J. Wash. Acad. Sci. 12: 367–86.
Steinhaus, E. A. (1940). 'The microbiology of insects....' Bact. Rev. 4: 17–57.
Stevenson, J. (1930). 'The Oligochaeta.' Oxford.
Stoklasa, J. & Doerell, I. L. C. (1926). 'Handbuch der biophysikalischen und biochemischen Durchforschung des Bodens.' Berlin.
Stoklasa, J. (1929). 'Die biochemischen Vorgänge bei der Humusbildung durch die Microorganismen im Boden.' Beitr. Biol. Pfl. 17: 272–96. [1930, Biol. Abstr. 4: 28791.]
Strickland, A. H. (1945). 'A survey of the arthropod soil and litter fauna of some forest reserves and cacao estates in Trinidad, British West Indies.' J. Anim. Ecol. 14: 1–11.

Süchting, H. (1929). 'Die Bekämpfung des Humus der Waldböden.' Z. Forst- u. Jagdw. 61: 349–63.

Sweetman, H. L. (1931). 'Preliminary report on the physical ecology of certain Phyllophaga (Scarabaeidae, Coleoptera).' Ecology, 12: 401–22.

Tamm, O. (1929). 'Die Bodentypen und ihre forstliche Bedeutung.' Proc. Int. Congr. For. Exp. Sta. (Stockholm): 449–54.

Taylor, E. McKenzie & Burns, A. C. (1924). 'Soil temperatures during the Sharaqi Period and their agricultural significance.' Bull. Minist. Agric. Egypt, 31: 1–46.

Taylor, E. McKenzie- & Williams, C. B. (1924). 'A comparison of sand and soil temperatures in Egypt.' Bull. Minist. Agric. Egypt, 40: 1–24.

Taylor, W. P. (1930). 'Animals a potent factor in soil formation.' Ecology, 11: 787–8.

Taylor, W. P. (1935*a*). 'Significance of the biotic community in ecological studies.' Quart. Rev. Biol. 10: 291–307.

Taylor, W. P. (1935*b*). 'Some animal relations to soils.' Ecology, 16: 127–36.

Thamdrup, H. M. (1932). 'Faunistische und ökologische Studien über dänische Oribatiden.' Z. Jb. Abt. 1. 62: 289–330.

Thiem, H. (1932). ['An interchangeable biological sieve.'] NachrBl. Dtsch. PflSchDienst. 12: 33–4.

Thomas, C. A. (1929). 'The parasites of wireworms (Coleop.: Elateridae).' Ent. News, 40: 287–93.

Thomas, C. A. & Horsfall, J. L. (1939). 'A method for studying the fauna of mushroom manure.' J. Econ. Ent. 32: 885.

Thompson, M. (1924). 'The soil population. An investigation of the biology of the soil in certain districts of Aberystwyth.' Ann. Appl. Biol. 11: 349–94.

Thorpe, W. H., Crombie, A. C., Hill, R. & Darrah, J. H. (1945). 'The food finding of wireworms (*Agriotes* spp.).' Nature, Lond. 155: 46–7.

Toumey, J. W. & Stickel, P. W. (1925). 'A new device for taking maximum and minimum soil temperatures in forest investigations.' Ecology, 6: 171–8.

Trägårdh, I. (1929). 'Studies in the fauna of the soil in Swedish forests.' Trans. 4th Int. Congr. Ent. 2: 781–92.

Trägårdh, I. (1933). 'Methods of automatic collecting for studying the fauna of the soil.' Bull. Ent. Res. 24: 203–14.

Trägårdh, I. & Forsslund, K. H. (1934). 'Studier över insamlingstekniken vid undersökningar över markens djurliv.' Medd. Skogsförsöksanst. Stockh. 27: 21–68.

Tullgren, A. (1917). 'En enkel apparat för automatiskt vittjande av sållgods.' Ent. Tidskr. 27: 97–100.

Ulrich, A. T. (1933). 'Die Makrofauna der Waldstreu. Quantitative Untersuchungen in Beständen mit guter und schlechter Zersetzung des Bestandesabfalles.' Mitt. Forstwirt. Forstwiss. 4: 283–323.

Uvarov, B. P. (1931). 'Insects and climate.' Trans. Ent. Soc. Lond. 79: 1–247.

Vestal, A. G. (1913). 'An associational study of Illinois sand prairie.' Bull. Ill. Lab. Nat. Hist. 10: 1–96.

Vinogradov, B. S. & Obolenskii, S. I. (1930). 'Injurious insects and other animals in the U.S.S.R. No. 5. Rodents (1925–8).' Works Appl. Ent., Leningr. 13: 257–324.

Volz, P. (1934). 'Untersuchungen über Mikroschichtung der Fauna von Waldböden.' Zool. Jb. (Abt. Syst.), 66: 153–210.

Waksman, S. A. (1927). 'Principles of soil microbiology.' London.

Waksman, S. A. (1938). 'Humus, origin, chemical composition, and importance in nature.' London. 2nd ed. revised.

Waksman, S. A. & Allen, M. C. (1932). 'Comparative rate of decomposition of composted manure and spent mushroom soil.' Soil Sci. 34: 189–95.

Waksman, S. A. & Gerretsen, F. C. (1931). 'Influence of temperature and moisture upon the nature and extent of decomposition of plant residues by microorganisms.' Ecol. 12: 33–60.

Waksman, S. A. & Starkey, R. L. (1924). 'Microbiological analysis of soil as an index of soil fertility: VII. Carbon dioxide evolution.' Soil Sci. 17: 141–61.

Waksman, S. A. & Tenney, F. G. (1927). 'The composition of natural organic materials and their decomposition in the soil. I. Methods of quantitative analysis of plant materials.' Soil Sci. 24: 275–83. Idem. 'II. Influence of age of plants upon the rapidity and nature of its decomposition.' Soil Sci. 24: 317–33.

Waksman, S. A., Tenney, F. G. & Stevens, K. R. (1928). 'The role of microorganisms in the transformation of organic matter in forest soils.' Ecology, 9: 126–44.

Walton, W. R. (1928). 'Earthworms as pests and otherwise.' Fmrs' Bull. U.S. Dep. Agric. 1569: 1–14.

Weaver, J. E. (1919). 'The ecological relations of roots.' Publ. Carneg. Inst. 286: 1–128.

Weese, A. O. (1924). 'Animal ecology of an Illinois elm-maple forest.' Illinois Biol. Monogr. 9: 345–437.

Wheeler, W. M. [1930]. 'Demons of the dust.' New York.

Wherry, E. T. (1924). 'Soil acidity preferences of earthworms.' Ecology, 5: 309.

Wigglesworth, V. B. (1939). 'The principles of insect physiology.' London.

Williams, A. B. (1936). 'The composition and dynamics of a beech-maple climax community.' Ecol. Monogr. 6: 319–408.

Williams, C. B. (1913*a*). 'The Berlese funnel.' Entomologist, 46: 273–4.

Williams, C. B. (1913*b*). 'A summary of the present knowledge of the Protura.' Entomologist, 46: 225–32.

Williams, E. C. (1941). 'An ecological study of the floor fauna of the Panama rain forest.' Bull. Chicago Acad. Sci. 6: 63–124.

Windred, G. L. (1933). 'Investigations on the Buffalo Fly *Lyperosia exigua* de Meij. Pt. IV. The influence of moisture on the larvae of *Lyperosia exigua*.' Pamphl. Coun. Sci. Industr. Res. Aust. 43: 23–40.

Wingate, W. J. (1906). 'A preliminary list of Durham Diptera with analytical tables.' Trans. Nat. Hist. Soc. Northumb. 2: 1–416.

Winogradsky, S. (1924). 'Sur l'étude microscopique du sol.' Comp. Rend. Acad. Sci. 179: 367–71.

Winogradsky, S. (1925). 'Études sur le microbiologie du sol. 1. Sur la méthode.' Ann. Inst. Pasteur, 39: 299–354.

Winogradsky, S. & Winogradsky, H. (1933). 'Études sur la microbiologie du sol. (Septième mémoire.) Nouvelles recherches sur les organismes de la nitrification.' Ann. Inst. Pasteur, 50: 350–432.

Wolcott, G. N. (1937). 'An animal census of two pastures and a meadow in Northern New York.' Ecol. Monogr. 7: 1–90.

Woodger, J. H. (1929). 'Biological principles. A critical study.' London.

Znamenskii, A. V. (1927). ['Instructions for carrying out observations on the entomofauna of the soil.'] Trans. Poltava Agric. Exp. Sta. 51: 1–58.

Van Zwaluwenburg, R. H. (1931). 'The soil fauna of sugar cane fields.' Chapter in: Handbook of the insects and other invertebrates of Hawaiian sugar cane fields by F. K. Williams. Exp. Sta. Hawaii Sugar Cane Planters Ass., Honolulu. Pp. 339–52.

REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 33, No. 2, 1946)

This number, of 208 pages, contains nine original papers and an account of *Gentiana pneumonanthe* by N. W. Simmonds, as part of the Biological Flora. There is also Professor A. R. Clapham's *Check List of British Vascular Plants*, the accepted names which are to be used in future numbers of the *Biological Flora* and *Journal of Ecology*. The original papers include the completion of A. S. Thomas's studies on hillside vegetation and biotic factors in Uganda and also an account of the Mora Forests of Trinidad by J. S. Beard. Dealing with ecology in Britain are two short papers by G. H. Locket on the colonization of bare chalk and on the water relations of chalk in relation to plants. John Wilkinson gives an account of the factors affecting the distribution of the Capreae group of *Salix* in the Gower Peninsula. Two papers deal with aquatic ecology. One is an account by R. W. Butcher of the algal growth in certain highly calcareous streams. The second is a full consideration of the distribution and status of *Glyceria maxima* in the Norfolk Broads, by J. M. Lambert. R. D. Tweed and N. Woodhead have reviewed and revised some of the conclusions drawn about *Juncus effusus* and *J. conglomeratus* in the *Biological Flora*. Dealing with methods is a paper by E. G. Pringsheim concerning the biphasic and soil-water culture methods for growing algae and flagellates.

There are four short reviews and a list of papers of ecological interest received. W. H. PEARSALL

TOLERANCE RANGE AND THE COMPOSITION OF COMMUNITIES

Ivar Agrell (1941). 'An objective method for characterization of animal and plant communities.' Förh. K. Fysiogr. Sällsk. i Lund, 15, No. 9: 1–15.

Ivar Agrell (1944). 'Zur Ökologie der Collembolen: Untersuchungen im Schwedischen Lappland.' Opusc. Ent. Suppl. 3: i–vi × 1–236.

The later paper describes the method used in the earlier work for the calculation of a tolerance or 'stenotopic-eurytopic' characteristic for the species of *Collembola* and for the various northern habitats (pine and birchwood litter, alpine meadow, heath and bog) in which they are found.

The 'characteristic number' of a species is the coefficient of variation (i.e. the standard deviation/mean) of the number of individuals of that species in a 'representative range of habitats' distributed throughout the area under investigation. This figure is claimed to measure, in some way, the extent of the animal's tolerance range in nature. Thus an animal present equally abundantly in all habitats studied has a characteristic number of zero, implying greatest possible tolerance, whilst a species which is present at 100% in one habitat only will have a characteristic number, denoted by 'v', of $\sqrt{(n-1)}$, where n = number of habitats studied. Evidently the greater the number of habitats studied, the higher will be 'v', so Agrell recommends the use of a 'relative characteristic number' ($= 100\, v/v_{max.}$) for comparing results when different numbers of habitats are studied. This parameter, when plotted against the relative dispersion of individuals in a region, gives a very similar curve to that obtained from the botanists' 'minimal area' index.

There are two outstanding difficulties in the way of applying this definition:

1. Measurement of the 'number of individuals'. This can be

(*a*) The actual number of individuals of the given species present in a standard sample: the 'abundancy number'.

(*b*) The actual number of individuals of the given species expressed as a percentage of the total individuals of all species: the 'dominancy number'.

(*c*) The percentage of samples, all taken from the same habitat, in which the species is present, expressed as a percentage of the number of samples taken. This is Agrell's and Shelford's 'constancy number'; Raunkiaer's and most European botanists' 'frequency'.

Agrell points out that the second figure, as an estimate of true population numbers, is liable to bias when some erratic factor accounts for a high proportion of an unusual species; in which case other species, present at normal density, will show an abnormally low dominancy number. The relative advantages of the use of abundancy as against constancy numbers will depend on the amount of time available for sampling and sorting the samples and on the information required. Agrell favours the use of constancy numbers in practice, which has the advantage that it admits of being expressed as percentage figures and demands much less careful counting of the samples, which can also be smaller. If abundancy figures have to be recorded in any case, a considerable amount of information will be wasted if constancy numbers only are derived from them. Abundancy measurements approach more closely an estimate of the true population numbers and will show up patchy distribution, whereas patchiness is liable to cause errors in determination of constancy numbers. On the other hand, derivation of abundancy numbers demands more labour in analysis of samples, which should also be large enough not to show great variances in the numbers recorded.

2. Variation in choice of habitats for sampling is the most obvious cause of discrepancy in the characteristic numbers attributed to species in the same area by different workers. Agrell himself uses the main macro-vegetation regions as his 'habitats' but, as his own work and also that of Hammer (1944, *Medd. Grønl.* 141, No. 3: 1–210) shows, there is little relation between the larger plants and the distribution of the Collembola. Moisture and the Cryptogam flora are much more important. Evidently it is necessary to make wide preliminary

investigations and to apply some 'objective' method for selecting habitats in terms of the Collembola fauna itself. Such a method is provided, Agrell suggests, by Kulczynski's technique (1927, *Bull. Int. Acad. Cracovie*, Suppl. 2: 57–204) which enables one to arrange a number of habitats in a linear series in which proximity in the list of habitats is dependent upon the extent to which species are shared in common. The method is laborious and not entirely satisfactory because it is evident that a linear series cannot adequately express the multi-dimensional affinities of a wide range of habitats; but it would probably allow one to decide which of a large number of 'subjective' habitats represent combinations of factors significant to the distribution of the Collembola and which could, with advantage, be combined.

The second half of the 1944 paper attempts to apply a similar method to habitats instead of to species. Two figures, based on *all* the species of Collembola in the whole area under investigation, are derived:

(*a*) The 'quantitative characteristic', the variance of the dominancy numbers of the species in the habitat under consideration. This figure is zero when all the species in the region are represented in equal proportions in the habitat in question, and, as in the case of the single species characteristic number, the figure is best expressed as the ratio of the actual quantitative characteristic to the maximum value obtainable with the number of habitats sampled $[=\sqrt{(n-1)}]$.

(*b*) The 'qualitative characteristic' or average of the characteristic numbers of species in the habitat, weighted by multiplying by dominancy numbers, so that a single dominant species scores a relatively high value.

Precise assessment of the meaning of these values is not easy. Both figures, over the range of habitats studied by Agrell, show parallel values, although the first, which seems to be more straightforward, shows more extreme values in peculiar environments, presumably because it is based on dominancy values only. The qualitative characteristic seems relatively more sensitive to absence of the more widespread species.

Assuming that the difficulty discussed under (*b*) above has been disposed of and that 'habitats' chosen are in some way representative of the range of environments in the area under study (and this difficulty has not really been faced by Agrell), can we attribute any meaning to the 'characteristic numbers' of individuals and communities? Agrell assumes, without attempting theoretical justification, that we can, and his own values do provide an empirical but consistent summary of the tolerance ranges of a species and of the 'peculiarity' or 'generality' of a habitat. Until the factor of choice of habitats by the investigator has been made less arbitrary we can, perhaps, hardly expect a more complete definition of these measurements. That they have even now a certain value is demonstrated by comparison with laboratory-determined tolerance ranges; and the method does seem to provide a means of tackling such very important problems as the comparison of spatial with temporal variations in animal numbers and the relation of 'stenotopy' or 'peculiarity' of an environment to its biomass turnover, thus providing a key to the construction of a more complete picture of the dynamics of the 'food chain'. At the same time the need for a thorough mathematical investigation of these and a great many more elementary problems connected with sampling is once more demonstrated.

A. MACFADYEN

A MODERN DESERT

R. S. R. Fitter (1945). *London's Natural History.* 282 pp., 12 text-figures, 41 plain and 52 coloured photographs. 'The New Naturalist,' Collins, 14 St James's Place, London, S.W. 1. Price 16*s*.

This useful monograph represents a considerable amount of research into the published history and natural history of London, as well as a good working knowledge of the different districts from first-hand visits. The book takes for convenience the area of land within twenty miles of St Paul's Cathedral, and traces the spread of urban influences upon wild life from early to modern times. 'In the centre of the area occupied by this vast community, the greatest that has ever been known on the face of the earth, is a solid core where hardly any of the soil ever sees the light of day.... Few plants except the ubiquitous mosses, and among animals only man's own commensals, such as sparrows, pigeons, rats, mice, spiders, flies, bugs, lice and cockroaches, are able to find a living in this desert of asphalt and brick.' Outside this central zone, as far as a dozen miles out, there is rather more opportunity for plants and animals to live, though urbanization is still intense, and ecological conditions much modified. Beyond that again town begins to interdigitate with country, mostly cultivated land.

Much of the wild-life interest comes, of course, in the surviving open spaces, as Parks and Forests. But even these are profoundly impoverished by the influence of man, who has worked out a peculiarly successful method of maintaining a certain scenic beauty of real charm by the use of a few trees, shrubs and grasses that can survive the impact of grazing, trampling, smashing, picking, and town smoke. Some of London's open spaces must be almost as impoverished in species of plants and animals as the Great Salt Lake or the High Arctic tundra, though perhaps not equally interesting ecologically, because the species that survive under man's heel are usually tough, widespread forms, not specialists in habitat. They survive because of immediate adaptability to these new and (on the evolutionary time scale) possibly ephemeral habitat conditions. As that eccentric genius A. H. Church wrote: 'A modern city with its fortuitous collection of human beings, may as readily dissolve again, and their rejectamenta be lost and buried under returning vegetation.'

The chief interest of this book to me was not so much in the records of interesting or local rarities that have turned up in London, and may form the legitimate targets of the person living there who is starved of real opportunities for studying nature, as in the history of changing equilibrium between wild life and man, and in some of the curious habitats and communities and changed habits that are to be found in the new conditions of this vast temperate desert. The historical description, succinctly written and well illustrated by maps and good quotations and examples, allows one to follow the gradual victory of bricks and mortar over nature. It evokes a half-

pleasant nostalgia for the days when wild hawks were encouraged to breed in Epping Forest—for the sake of hawking (precursor of small arms, whose use turned the hawk from an essential asset into a reputed enemy of sportsmen); and when the Thames was a salmon river, abounding also in other species of fish (the salmon did not continue after 1833).

Among special habitats which have attracted new though limited communities of their own, adapted to urban life, are sewage filters, hot-houses, stored products such as cereals (with their strange mixture of tropical and British species), the 'cliffs' formed by large buildings (with bird populations such as pigeons, starlings, and the black redstart—a recent colonist), and man himself with his insurgent ectoparasites and endoparasites. These points the author notices, but without citation of the comparatively rich technical knowledge that now exists, except that he deals fairly with the birds, e.g. with the changed habits of the black redstart and the black-headed gull.

Mr Fitter does not bring out, perhaps, how little we know about even the impoverished animal communities of urban areas. For where can one find a thorough survey of the complete animal life of a house or a garden, or even of the stored foods upon which so much specialized population study has been focused in recent years? The very simplicity of structure of these communities might encourage systematic investigation by ecologists.

As regards format, this book is well printed and supplied with a bibliography (with names and dates) for each chapter. The main list of references has unfortunately omitted some of the chapter references, including one of the author's own papers. The numerous illustrations will doubtless appeal to the uncritical reader; but the half-tones are poor in quality and their subjects fairly commonplace. Of the coloured plates, the less said the better: if the publishers consider that a new but equally arbitrary conventional portrayal of the colours of reality is preferable to one done in black and white, they have succeeded in supplying it. The Appendices contain various useful plant and animal lists, also a register of natural history societies and museums. The naturalist living in any large city will find this book full of suggestions and topics for research. C.E.

TEXT-BOOKS ON PLANT ECOLOGY

(*a*) **A. G. Tansley (1946).** *Introduction to plant ecology.* 260 pp. and 17 text-figures. George Allen and Unwin Ltd., 40 Museum Street, London, W.C. 1. Price 8*s.* 6*d.*

(*b*) **A. G. Tansley & E. Price Evans (1946).** *Plant ecology and the school.* 97 pp. and 10 text-figures. George Allen and Unwin Ltd. Price 6*s.*

(*a*) The larger of these two books is a partly re-written version of Professor Tansley's valuable 'Practical plant ecology', originally published in 1923 and since then twice re-issued. It is an excellent thing that students should have a text-book that contains the latest views by a very great authority on the ecology of plant communities. The important place of semi-natural vegetation in the British scene is given prominence. A balanced summary of vegetation structure and succession leads on to a brief review of British plant formations, after which there are notes on the methods of field survey, with transects, quadrat work and other tools of the plant ecologist. After this, habitat factors are defined and methods of measuring atmospheric, soil and biotic factors detailed. In connexion with biotic factors, there is a statement of the ideas of biome and ecosystem—and a plea for co-operative research between plant and animal ecologists 'to elucidate such relations as those described, and others which must certainly exist, many of them probably still unsuspected'. The book concludes with a discussion of nature study in schools and suggestions for continuation work; though one is still doubtful how far true experimental science can profitably be taught below almost University level of training. The bibliography, arranged under main subjects, is an excellent introduction to the literature, and includes many regional studies in Britain, as well as nine papers on biotic and human factors.

(*b*) The smaller book for schools starts from familiar ideas in geography to explain the role of vegetation in forming landscape and interspersed plant formations and communities. Again, the influence of man and animals is underlined, and it is noted that 'the fact that any particular plant community is not entirely spontaneous but owes its present condition partly to human agency, is far from destroying its suitability and interest for ecological study, provided the human factors are taken into full account'. Such advice is realistic for children growing up in a country so closely occupied as ours, and it corrects a certain one-sidedness noticeable in Professor Tansley's great monograph on British vegetation, with its main emphasis on the naturalness of many British plant communities. On the other hand, it is to be hoped that teachers will find opportunity in their practical ecology work to draw attention to the special interest and charm of natural wild life and the dangers of destruction or modification which beset it nowadays.

The authors suggest a 'golden rule' of 'observation first, then concepts, followed by terms and definitions'. All ecologists please copy! There is much other wisdom and sound advice about the approach to field studies and technical methods. Forty-five pages of the book are applied to fairly detailed descriptions of the chief plant formations: woodland, scrub and hedge, grassland, heath and moor, fresh water, water margin, salt marsh, sand dune and shingle, and arable field. For each the whole ecosystem is indicated and the lucid and fruitful style should attract many readers. There is a semi-philosophical chapter in conclusion, bringing out the values in education to be derived from ecological study. C.E.

FIELD NATURAL HISTORY

A. W. Boyd (1946). *The country diary of a Cheshire man.* 320 pp. and 19 half-tone photos. Collins, 14 St James's Place, London, S.W. 1. Price 12*s.* 6*d.*

The daily 'Country Diary' in the *Manchester Guardian* has always kept a high standard, and its intelligent and pleasant treatment of nature has been in favourable contrast to the hack work and jejune, complacent out-

pourings of most popular natural history. Mr Boyd has contributed weekly notes in this series since 1933, and they have always struck me as especially noteworthy for their fresh and objective outlook, and the range of their interest, from birds and moths and flowers to folk-lore and the endemic language of Cheshire. The reprinting of over 500 of these items in the form of a book, illustrated by modest photographs of habitats and some of their animal and plant species, will now enable a great many naturalists who do not happen to be Liberals to follow his seasonal diary of wild-life events in a North of England county. The general picture produced is like the kind that some artists paint with a palette knife—it is built up of innumerable small units, and therefore needs to be focused rather carefully.

Cheshire, outside its industrial patches with which the author hardly deals, is predominantly pasture and ploughed fields, but with some hills, patches of 'moss' in the stream valleys, heaths as in Delamere Forest, and a little coast land. But the glory of Cheshire's wild habitats is its meres, lying in glacial ground or in the 'flashes' formed by subsidence over salt mines. The wild-fowl of these meres, both resident and migrant, are one of the chief themes of these notes. But a vast number of other topics occur, and all are obviously the fruit of actual field watching, supported by reports from other observers likely to be reliable.

This book affords an opportunity for considering how far work of this kind is valuable to science. I think, to begin with, it is first-class educative stuff, for it interests the public in their living surroundings and encourages the general sympathy without which conservation cannot be more than a legal dead-letter. To gain this support by honest and obviously first-hand description is in itself a victory, for there is danger of the public's reaction to wild life being only sentimental or else poisoned by attitudes of ownership rather than trusteeship. And ecologists are beginning to understand that the animal and plant communities that contain the materials for their research and experiment may disappear unless conservation quickly becomes an executive reality.

I should say that a book like this will probably irritate a fair number of those ecologists who are not interested in nature as a whole. That is another good thing, in so far as oysters may be expected to produce pearls. At any rate, it is surely good to be reminded that ecological study aims at a working description and analysis of the total ecosystem of the world, and that the highest abstractions should keep in touch with reality. On this point we must mention the curious fact known to most professional animal ecologists, that the very richness of their subject prevents them from easily remaining out of doors for more than a fraction of their working time: they are hauled away by the demands of specimen study, note copying, analysis and literature, not to mention teaching. All the more advantage if we can keep a line open to the field naturalist and the kind of patient field observation that he is most likely and able to make.

It cannot be denied, however, that a book like Mr Boyd's is for browsing and associative reflection, rather than straight reading; but it can be strongly recommended, and is on the highest level of amateur work. For those who want hard facts to use, there is an index of the species mentioned.

The author has personally aroused the interest of and helped to train a very large number of naturalists in the counties round him, as well as conducting a number of scientific inquiries into population problems in birds. This might be illustrated perhaps by his own story of the urchin, pressed by his companions to come and play, who replied, 'Naw, I'm watchin' this feller spyin' out.' It is good that field ecology can be infectious. C.E.

A CORRECTION

Ellsworth Huntington. *Mainsprings of civilization.* (Reviewed in this Journal, 1946, Vol. 15, pp. 105–6.)

The Editors regret that one or two words in a quotation were wrongly copied from the reviewer's MS. The reviewer has asked us to mention that he incorrectly interpreted some statements by Prof. Huntington as indicating a belief in Lamarckism. This error arose from the ambiguity sometimes attaching to the use of metaphor in describing evolutionary processes. Prof. Huntington does not believe in the inheritance of acquired characteristics.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, 91 Banbury Road, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by H. F. Barnes, D. Chitty, A. C. Evans, E. M. O. Laurie, E. Nelmes, F. T. K. Pentelow, W. S. Richards, M. R. Shorten and H. N. Southern; checking by B. M. Hobby.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Burke, F. (1946). 'Mosquito fauna of some Cheshire saline waters.' Ent. Mon. Mag. 82: 228–30.

List of mosquitoes associated with brine pits in Cheshire, together with the concentration of sodium chloride and total salts in those pits. In particular a second breeding area found for *Aëdes dorsalis* and four inland stations for the coastal, brackish water form *A. detritus*.

Stephenson, W. (1941). 'An ecological survey on a beach on the Island of Raasay.' Proc. Univ. Durham Phil. Soc. 10: 332–57.

The distribution of the dominant algae, commoner burrowing animals, commoner surface living animals and the succession of species is noted in terms of percentage exposure. Critical levels of distribution for the commoner burrowing animals occurred at exposure levels of 0, 10, 20 and 50%; and for surface living animals at 10%, about 25 and 50%. The critical levels appear largely independent of changes in the dominant algae at different levels. Animals living under stones are also considered.

(*b*) Fresh water

Attlee, H. G. (1946). 'Odonata in 1945.' Entomologist, 79: 34–6.

Notes on dates of occurrence with localities of dragonflies in south-east England.

Beirne, B. P. & Harris, J. R. (1946). 'Light-trap captures in Ireland in 1945 (Lep., Trich., Ephem., Plec.).' Ent. Rec. 58: 46–9.

Details of catches of moths, caddis flies, mayflies and stoneflies in two light traps operating in 1945, one in the valley of the Liffey at Lucan (Éire) and the other on the cliffs of Howth (Éire).

Brown, E. S. (1946). 'The variation of *Glaenocorisa* Thomson (Hemipt., Corixidae) in the British Isles, and its probable cause.' Trans. R. Ent. Soc. Lond. 96: 1–10.

The colour-tone of the background over which the insects live is the main factor responsible for determining the colour of *Glaenocorisa*. There is thus no reason for accepting *G. cavifrons* and *G. propinqua* as subspecies. The 'cline' is a local one dependent upon graded differences in habitat-type.

Brown, M. E. (1946). 'The growth of brown trout (*Salmo trutta* Linn.) I. Factors influencing the growth of trout fry'. J. Exp. Biol. 22: 118–29. 'Idem. II. The growth of two-year-old trout at a constant temperature of 11·5° C.' J. Exp. Biol. 22: 130–44. 'Idem. III. The effect of temperature on the growth of two-year-old trout.' J. Exp. Biol. 22: 145–55.

A detailed study of the growth of trout under controlled conditions.

Collinge, W. E. (1945). 'Notes on the British freshwater Isopoda, No. 1.' Northw. Nat. 20: 149–53.

Includes descriptions of a new species, *Asellus patoni*, and two varieties of it (*nigrescens* and *maculata*) from Mitcham Common, Surrey; instructions for keeping *A. aquaticus* in captivity; and additional distributional records for *A. meridianus* in Yorkshire, Westmorland, Devon, Kent and Cumberland.

Edmondson, T. (1945). 'The birds of Pennington Flash, South Lancashire.' Northw. Nat. 20: 183–91.

Notes dealing chiefly with the abundance and habitats of birds observed at Pennington Flash, mostly between 1939 and 1944, preceded by a description of the topography of the lake.

Ellison, N. F. (1945). 'Note on *Corixa* flying.' Northw. Nat. 20: 272.

On 2 October 1945 large numbers of *C. geoffroyi* alighted on wet tar, which they evidently mistook for the reflexion of the sun on water, at West Kirby. The nearest pond was about ½ mile away.

Hill, A. R. (1946). 'A short account of Plecoptera in the Tay basin area, Scotland, with notes on their ecology.' Ent. Mon. Mag. 82: 233–4.

Notes on the distribution, habitat and mode of life of 20 species of stoneflies found in the Tay basin.

Killington, F. J. (1946). 'Mosquitoes in the Poole district.' J. Soc. Brit. Ent. 3: 35–6.

Notes on the ecology and distribution of 13 species of mosquitoes found in the Poole district. *Anopheles claviger*, *Aëdes punctor* and *A. detritus* are serious pests. *Anopheles maculipennis* var. *atroparvus* and *A. claviger* are potential malaria carriers.

Pearsall, W. H., Gardiner, A. C. & Greenshields, F. (1946). 'Freshwater biology and water supply in Britain.' Sci. Publ. Freshw. Biol. Ass. Brit. Emp. No. 11: 1–90. (Price to non-members, 4*s*. Freshwater Biological Association, Wray Castle, Ambleside, Westmorland.)

The chief biological principle of water supply management is to keep the fertility of the water low in order to reduce the work of removing the various forms of life into which organic matter is converted. Thus a reservoir should be deep enough to support the minimum amount of higher aquatics, and anaerobic conditions should be avoided since they cause the liberation of nutrients from the mud and deposits by iron-bacteria of ferric compounds in the mains. These and other principles are fully discussed in a lucid manner.

Watson, J. M. (1944). 'Studies on the morphology and bionomics of a little known holotrichous ciliate—*Balantiophorus minutus* Schew. Part II. The effect of environmental factors.' J. R. Micr. Soc. 64: 31–67.

This ciliate can remain fully active in very restricted films of water and can tolerate a wide range of temperatures and *p*H. Anabiosis and encystation are described.

(*c*) Land

Allan, P. B. M. (1945). 'Lepidoptera seen in Montgomeryshire, 1941–1945.' Northw. Nat. 20: 175–82.

A list of 288 Macrolepidoptera observed, caught or reared in a district 2–5 miles west of Newtown, with a further list of 13 species caught at an altitude of 1200–1500 ft. in the Plynlimmon district in 1938.

Allan, P. B. M. (1945). 'The oak hook-tip in North Wales.' Northw. Nat. 20: 259.

Two males and a female of the moth *Drepana binaria* were seen in Montgomeryshire on 29 July 1945 about a mile from the place where this species was recorded in 1943.

Blair, K. G. (1946). 'Notes from freshwater, I.W., including a wainscot (Lep., Agrotidae) new to Britain.' Ent. Mon. Mag. 82: 140–1.

Records from the great reed beds at the mouth of the Yar, in particular the central and east European moth *Sedina büttneri* Herring (new to Britain) and other fen species of moths.

Bowden, J. (1946). '*Lispe superciliosa* Lw. (Dept., Muscidae) new to Britain.' Ent. Mon. Mag. 82: 211–12.

Probably from damp soil near a pig mud wallow. Differences between this species, *L. litorea* and *L. loewi* discussed.

Easton, A. M. (1946). '*Apion lemoroi* Brisout (Col., Curculionidae), a species new to Britain.' Ent. Mon. Mag. 82: 130–1.

Found in stems of and by sweeping *Polygonum aviculare* near Effingham, Surrey. A Braconid parasite of the genus *Sigalphus* was associated with it.

Freeman, R. B. (1946). 'Coleoptera from the nest of the robin.' Ent. Mon. Mag. 82: 217.

38 species of beetles from 20 nests built on the ground in Wytham wood, Berkshire. The list includes ground- and refuse-dwelling species together with typical nest inhabitants.

Grensted, L. W. (1946). 'An assemblage of Diptera on cow-parsnip.' Ent. Mon. Mag. 82: 180.

Captures made in September on Dartmoor above Bridstowe at 950 ft. 37 species of Diptera recorded, Syrphids dominant.

Griffith, C. F. (1945). '*Liodes picea* Ill. and *Grynobius kiesenwetteri* Edw. in North Lancashire.' Northw. Nat. 20: 259.

The Anobiid beetle *G. kiesenwetteri* is recorded from Lancashire for the first, and the Anisotomid *L. picea* for the second, time.

Griffiths, W. & Wilson, W. (1945). 'The birds of North Wirral.' Northw. Nat. 20: 164–74.

This annotated list of 72 species concludes the series.

Harrison, J. W. Heslop (1946). 'The distribution of *Zygaena purpuralis* and *Z. filipendulae* in the Hebrides.' Entomologist, 79: 65.

A reply to a note by J. L. Campbell (1945, *Entomologist* 78: 20) on the distribution of these burnet moths.

Heath, J. (1946). 'Notes on some Lepidoptera from the Falmouth district of south Cornwall.' J. Soc. Brit. Ent. 3: 13–18.

Notes on the distribution and abundance of 131 species, including 22 new district records and 6 new county records.

Henderson, J. L. (1946). 'More beetles of a London suburban garden in Surrey.' Ent. Mon. Mag. 82: 38–9.

List and points of interest of 43 additional species of beetles, bringing the total number recorded for that area to 366.

Hobby, B. M. (1946). 'A further instance of "anting" by a starling.' Proc. R. Ent. Soc. Lond. A, 21: 2.

The ant involved was *Acanthomyops mixtus*.

Kaufmann, R. R. U. (1946). '*Asemum striatum* L. (Col., Cerambycidae) in Cheshire.' Ent. Mon. Mag. 82: 198.

Has become established in Scots pine in Cheshire—new locality.

Kaufmann, R. R. U. (1946). 'The distribution of *Prionus coriarius* L. (Col., Prionidae) in Great Britain.' Ent. Mon. Mag. 82: 251–2.

This longicorn beetle appears to be restricted to a zone stretching from Gloucestershire to Lancashire, and a zone extending all along the coast from Land's End to Norfolk. This information appears incomplete and the two zones may join up via Nottingham.

Killington, F. J. (1946). 'On *Psectra diptera* (Burm.) (Neur., Hemerobiidae) including an account of its life-history.' Ent. Mon. Mag. 82: 161–76.

Only twelve British localities known, but has been recorded from England, Scotland and Éire. Occurs in north-west Europe and north-east America, but is rare everywhere probably owing to its inconspicuous appearance. Adult and larvae are predacious and live in damp, rank herbage. The micropterous form has a characteristic hop. The morphology of egg, larval, pupal and adult stages is described in detail. The adult is active from June to September. Sixty-four eggs were laid in small batches by a single female. They took 13–16 days to hatch. Larvae probably overwinter in the third (last) instar. The larva then spins a cocoon, changes into the pupa in about a week and thus becomes adult the following week.

Lancum, F. Howard (1946). 'Wild birds and agriculture. 3. The owls.' J. Minist. Agric. 53: 133–5.

The barn, tawny, long-eared, short-eared and little owls.

Lancum, F. Howard (1946). 'Wild birds and agriculture. 4. The doves.' J. Minist. Agric. 53: 184–6.

Ring-dove or wood-pigeon, stock-dove, rock-dove and turtle-dove.

Lancum, F. Howard (1946). 'Wild birds and agriculture. 5. The thrushes.' J. Minist. Agric. 53: 225–7.

Song-thrush, mistle-thrush, blackbird, fieldfare and redwing.

Lancum, F. Howard (1946). 'Wild birds and agriculture. 6. The cuckoo.' J. Minist. Agric. 53: 270–2.

Lancum, F. Howard (1946). 'Wild birds and agriculture. 7. The woodpeckers.' J. Minist. Agric. 53: 316–18.

The green, great spotted and lesser spotted.

Lancum, F. Howard (1946). 'Wild birds and agriculture. 8. The tits.' J. Minist. Agric. 53: 369–71.

The great, blue, coal and long-tailed tits.

La Touche, A. A. D. (1946). 'Hampshire spiders including the description of a new species, *Diplocephalus cottoni*.' Proc. Zool. Soc. Lond. 115: 281–95.

A list of species from five localities in the south of Hampshire including the New Forest.

[Lloyd, B.] (1945). 'Notes on the mammals of Pembrokeshire. Extracted from the journals of Bertram Lloyd.' Northw. Nat. 20: 233–44.

Records of some 27 species observed between 1925 and 1940, with localities and notes on the abundance of many and the habits of some.

Lloyd, B. (1945). 'Census of Pembrokeshire reptiles and amphibians.' Northw. Nat. 20: 258–9.

Records of four reptiles and three amphibians, with some indications of abundance.

McMillan, N. F. (1945). 'Butterflies swarming on Michaelmas daisies.' Northw. Nat. 20: 260.

In a garden in Cheshire in which large numbers of butterflies were congregated on Michaelmas daisies, 41 small tortoiseshells (*Aglais urticae*), three red admirals (*Vanessa atalanta*), two whites (*Pieris*) and one peacock (*Nymphalis io*) were observed on one clump. Only varieties with red-mauve flowers were visited, those with white or pale blue-mauve flowers being ignored.

Niblett, M. (1946). 'British Trypetidae.' Ent. Rec. 58: 6–8.

Detailed notes on the life history, ecology, host plant and distribution of 15 species of British Trypetid flies.

Niblett, M. (1946). 'Diptera bred from flower-heads of Compositae.' Ent. Rec. 58: 121–3.

Notes on ecology and distribution of 9 species of flies.

Payne, L. G. (1945). '*Phyllobius artemisiae* Desbr. A new county record.' Northw. Nat. 20: 270–1.

This weevil, hitherto known in England only from Kent and Cumberland, is recorded from Yorkshire, where it was found on a sandy area near Doncaster and on flood refuse near Kelfield.

Ruttledge, R. F. (1946). 'Roosting habits of the Irish coal-tit, with some observations on other habits.' Brit. Birds, 39: 326–33.

Notes are given on the type of roosting place preferred by this species (*Parus ater*), on the times of roosting in relation to sunset and weather, on the degree to which individuals are sedentary (a diagram shows the distribution of observations of a marked bird for 23 months), etc.

Sharpe, J. S. (1946). 'A few Coleoptera of western Merionethshire.' Ent. Mon. Mag. 82: 203–5.

Partial list of 170 species with notes on habitat. Merionethshire contains a very varied selection of habitats ranging from sea level sand dunes and marsh, to moorland of over 1000 ft. in altitude.

Sibson, R. B. (1945). 'Notes on birds of Sandbach, S.E. Cheshire.' Northw. Nat. 20: 247–55.

Contains notes on the abundance, distribution and habits of 60 species observed between September 1935 and July 1939 on dairy-farming land with some arable land and copses in south-east Cheshire. A map shows regular breeding sites of the willow-tit (*Parus atricapillus*) and places where it has been observed in winter, localities where the corncrake (*Crex crex*) has been heard, and breeding sites of the grasshopper warbler (*Locustella naevia*).

Simms, R. B. (1945). 'Notes on the past and present distribution of some Orthoptera in the south level of the E. Anglian fenland: with a particular study of *Tettigonia viridissima* L. and *Conocephalus dorsalis* (Thunb.) (Orthopt., Tettigoniidae).' J. Soc. Brit. Ent. 2: 252–73.

Drainage of the fens and the absence of hedges has caused the diminution or extinction of several hygrophilous Orthoptera, e.g. *Mecostethus grossus*. *Pholidoptera griseoaptera* is absent for no apparent reason (possibly climate or geology). In contrast, *Tettigonia viridissima* and *Conocephalus dorsalis* are still well established. In the former, survival is due to its favouring rather dryer ground, and to the existence of wide grassy verges to the 'droves' suitable for oviposition, associated with a tall and dense growth of burdock (*Arctium lappa*) which affords suitable cover for the relatively large and clumsy males. In *C. dorsalis*, survival is due to the power of maintaining colonies in small areas of rank vegetation and in particular to protective resemblance to rushes, grasses and sedges and to endophytic oviposition in *Juncus* and possibly in other monocotyledons. (This last renders it susceptible to reed cutting or grazing.)

Staton, J. (Ed.) (1946). 'Report on the birds of Nottinghamshire for 1945.' Nottingham Natural Science Field Club and the Trent Valley Bird Watchers. 36 pp.

Notes on the breeding of the black-winged stilt (*Himantopus himantopus*) on a sewage farm; and scattered records about other birds.

Thomas, I., Brown, E. B. & Willis, R. J. (1946). 'The cereals root eelworm, *Heterodera major* (O. Schmidt) Franklin, in North Wales.' Ann. Appl. Biol. 33: 63–5.

Local distribution of this nematode in North Wales.

Townsend, C. C. (1946). 'Insects observed in a Cornish tin mine.' Ent. Mon. Mag. 82: 197–8.

Conditions varied from cold and damp to 130° F. The fly (*Sciara* sp.) was probably breeding in stacks of rotten timber, the cockroach (*Blatta orientalis*) probably maintained itself on crumbs from miners' lunches; the Collembola *Sinella cocca* (a greenhouse species) was found in and around latrines in the warmest section of the mine; the longhorn beetle *Tetropium gabrieli* probably breeds in pit-props in small numbers.

Townsend, C. C. (1946). 'Cornish Coleoptera in 1945.' Ent. Mon. Mag. 82: 244–5.

Notes on distribution and ecology of about 60 species of beetles of a rare or local interest.

(*d*) Small islands

Campbell, J. L. (1946). 'Catalogue of a collection of macro-lepidoptera made in the Hebrides between 1936 and the present date.' Entomologist, 79: 49–53.

Locality records and habitat classifications of 177 species, mainly caught on Barra and Canna, with a few records from other neighbouring islands.

Cowin, W. S. & Williamson, K. (1946). 'Manx Diptera.' Ent. Mon. Mag. 82: 121.

47 additional records of manx flies including a new locality on Ballaugh Curragh for the rare Asilid *Pamponerus germanicus*.

Day, F. H. (1945). 'Records of Coleoptera from the Orkney Isles.' Northw. Nat. 20: 271–2.

A list of 57 species belonging to nine families collected on three islands in 1943–5, with some indications of abundance. Stated to be of interest only as a record of recent occurrences.

Perkins, J. F. (1946). '*Ephialtes diversicostae* Perkins and *Pimpla arctica* Zett. (Hym., Ichneumonidae) new to Britain.' Ent. Mon. Mag. 82: 206.

Pimpla arctica is an Arctic and alpine form, here recorded from the Isle of Soay.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Barnes, H. F. (1946). 'Gall midges of economic importance.' Vol. I. 'Gall midges of root and vegetable crops.' 104 pp., 6 plain & 4 coloured plates. Vol. II. 'Gall midges of fodder crops.' 160 pp., 3 plain & 1 coloured plate. Crosby Lockwood and Son, Ltd., 20 Tudor Street, London, E.C. 4. Price 12*s*. 6*d*. & 15*s*. respectively.

These two books, which are to be followed by other volumes dealing with the gall midges (Cecidomyiidae) of fruit, ornamental trees and shrubs, trees, cereals, etc., are not primarily taxonomic. They describe what is known about the galls produced by different species of midges (although in a good many cases the species themselves have not been identified), but do not give much information about the actual taxonomy of the midges themselves. (It seems carrying popular presentation rather far, in what are really very technical publications, to mention the word 'Cecidomyiidae' once at the beginning of Vol. I and not at all in the early part of Vol. II.) The information, summarized from a large literature and from the author's considerable collections and field and insectary observations, is very valuable to ecologists, and includes descriptions of types of damage, geographical distribution, life history and food plants, enemies and parasites, and control methods. The arrangement is under plant groups and species, and is world-wide in scope, not confined to British crop plants. There are large reference lists, and three indexes dealing with gall midges, plant hosts and general subjects.

Collin, J. E. (1946). 'The British genera and species of Oscinellinae (Diptera, Chloropidae).' Trans. R. Ent. Soc. Lond. 97: 117–48.

Tables of genera and species with a few notes on their host plants.

Cooper, B. A. (1946). 'The larvae of *Corymbites nigricornis* Panz., *C. impressus* F., and *Athous difformis* Lac. (Col., Elateridae).' Ent. Mon. Mag. 82: 178–80.

Further emendations to Van Emden's key to the British Elaterid larvae 1945, Ent. Mon. Mag. 81: 20.

Edney, E. B. (1946). 'An apparatus for handling small living insects.' Bull. Ent. Res. 37: 83–7.

An apparatus based on air filter pumps useful for the examination of living fleas and other small insects.

Hickin, N. E. (1946). 'Larvae of the British Trichoptera. 22.' Proc. R. Ent. Soc. Lond. A, 21: 55–60.

Full description of the case and larva of the caddis fly *Molanna angustata*.

Hickin, N. E. (1946). 'Larvae of the British Trichoptera. 21.' Proc. R. Ent. Soc. Lond. A, 21: 61–5.

Full description of the case and larva of the caddis fly *Glyphotaelius pellucidus*.

Kevan, D. K. (1946). 'The sexual characters of the British species of the genus *Choleva* Lat., including *C. cisteloides* Fröhl. new to the British list (Col., Cholevidae).' Ent. Mon. Mag. 82: 122–30.

A key to the British species of *Choleva* is given, together with notes on habitat. Seven species are almost exclusively subterranean, *C. cisteloides* flies on warm days and can be caught by sweeping.

Orton, J. H. (1946). 'Biology of *Patella* in Great Britain.' Nature, Lond. 158: 173–4.

The recognition of at least three species of limpet (*Patella*) in the south of England by Fischer-Piette in 1935 renders all special observations on *Patella vulgata* prior to this date subject to revision. This note especially reviews new observations on those sex phenomena in *Patella* noted by Orton in 1928.

Richards, O. W. (1946). 'On the identity of the British sand-wasp hitherto known as *Ammophila campestris* Latr. (Hym., Sphecidae).' Ent. Mon. Mag. 82: 235.

All British specimens belong to *A. pubescens* (=*A. adriaansei*) (preying on caterpillars). *A. campestris* (preying on sawfly larvae) is only recorded from Jersey, but may occur in eastern England. Differences between species are tabulated.

Steel, W. O. (1946). 'On *Xantholinus distans* Muls. and Rey and *X. cribripennis* Fvl. with notes on other British species of the genus (Col., Staphylinidae).' Ent. Mon. Mag. 82: 192–5.

Description and localities for these, and a key to British *Xantholinus* spp.

Tetley, H. (1945). 'Notes on British polecats and ferrets.' Proc. Zool. Soc, Lond. 115: 212–17.

Examination of ferret skulls suggests that they have been derived from both the present British races of polecat, *Putorius p. anglius* and *P. p. caledoniae*.

Turk, F. A. (1945). 'Myriapodological Notes, I.' Northw. Nat. 20: 137–44.

Includes the first record of *Lithobius nigrifrons* and *Polydesmus denticulatus* from Cornwall; a revised key to the British Lithobiids and one to the British species of *Polydesmus*; a description of atypical nests constructed by Polydesmids, probably *P. angustus*, on a heap of large stones that formed the floor, of which two were connected by a covered way 2 mm. high and 12–15 mm. long and one contained 11 eggs; a list quoted from the files of the Speleo-biological Section of the British Speleological Association of the records to date of the five Diplopoda taken in English caves (including one for *P. coriaceus*, believed to be the first for this species from a cave, and an additional locality in Somerset for *Polymicrodon polydesmoides*); and evidence suggesting that the presence in large numbers of *Cylindroiulus punctatus*, which is the commonest Myriapod in Cornwall, in districts where there is little woodland indicates that the latter was formerly more extensive.

Wollaston, H. J. Buchanan- (1945). 'On statistical treatment of the results of parallel trials with special reference to fishery research.' Sci. Publ. Freshw. Ass. Brit. Emp. No. 10: 1–55. (Price to non-members 2*s.* 6*d*. Freshwater Biological Association, Wray Castle, Ambleside, Westmorland.)

Independent parallel trials are dealt with inadequately in most statistical text-books. In this paper techniques and probability tables are given for testing the null hypothesis that in two sets of trials there is equal likelihood of an event occurring as often in one as in the other.

3. PARASITES

Arthur, D. R. (1946). 'On *Megasella rufipes* Meigen in relation to the tick, *Ixodes ricinus* L.' Entomologist, 79: 132–4.

Normal healthy ticks are not subject to attack by the immature stages of the Phorid fly *M. rufipes*, but when conditions become unfavourable so that death of the tick ensues, the subsequent introduction of the dipterous larvae may result in a high degree of saprophytism.

Beirne, B. P. (1946). 'Notes on the biology of some Hymenopterous parasites of the beech weevil (*Rhynchaenus fagi* L.) (Col.).' Proc. R. Ent. Soc. Lond. A, 21: 7–11.

Of 900 weevil larvae of *Rhynchaenus fagi* collected at Foxrock, Co. Dublin in 1941 only 22% produced adult weevils, 44% were parasitized by the Braconid *Triaspis pallidipes* and 22% by the Braconid *Colastes braconius*. Other causes accounted for 12% of which more than half were killed apparently by a species of yeast.

Carpenter, G. D. Hale (1945). 'Bionomic notes on a colony of *Zygaena filipendulae* L. (Lep.).' J. Soc. Brit. Ent. 2: 280–5.

2564 cocoons of *Zygaena* sp. from a road verge 100 × 2 yd. were collected in 1944 from which insects emerged between 4 June and 17 August 1945. 133 cocoons were found empty, 706 failed to produce any insects, 5 produced *Z. lonicerae*, 979 produced live *Z. filipendulae* imagos, 463 contained parasitized dead *Z. filipendulae* pupae. The primary parasites were: DIPTERA: *Phryxe longicauda*, 78 (specific for *Zygaena*); *Neopales pavida* Mg., 91; HYMENOPTERA: *Casinaria orbitalis*, 118; *Gambrus* sp., 2; *Apanteles zygaenarum*, 30; *Habrocytus trypetae*, 5. Secondary parasites were the Hymenoptera: *Gelis instabilis*, 22; *Gelis* sp., 3; *Itoplectis maculator*, 10; and *Hemiteles nana*, 13. Only one parasite emerged from each cocoon save one which yielded 4 *A. zygaenarum* and 4 *C. orbitalis*. Several cases of attack by birds in the field were noted. In many cases the contents were rejected when the cocoon was opened. Attack was most severe on cocoons in exposed positions at the height of the fledgeling season.

Doncaster, J. P. & Kassanis, B. (1946). 'The shallot aphis, *Myzus ascalonicus* Doncaster, and its behaviour as a vector of plant viruses.' Ann. Appl. Biol. 33: 66–8.

This aphis, whose summer habits and hosts are unknown, has been found on shallots in storage and on onions and other species of plants both in glasshouses and in the open between October and June. Superficially similar to *M. persicae*, it differs morphologically and in its ability to transmit various viruses but not others.

Freeman, R. B. (1946). '*Pitrufquenia coypus* Marelli (Mallophaga, Gyropidae), an ectoparasite on *Myocastor coypus* Mol.' Ent. Mon. Mag. 82: 226–7.

Parasite only recorded from South America (Chile) on the coypu, now found on feral specimens caught in Norfolk.

Killington, F. J. & Bathe, E. C. (1946). 'Acarine parasites of Odonata. I.—*Leptus* (*Ochorolophus*) *killingtoni* Turk.' Ent. Mon. Mag. 82: 257–66.

Details of infestation of 170 *Leptus* on 118 dragonflies, namely *Pyrrhosoma nymphula* and *Enallagma cyathigerum*, on Alderney Heath, Dorset. Attachment is by the mandibles, no particular part of the body is selected. The mite is not restricted to dragonflies, but has been found on aphides on a *Hemerobius* sp. Found only in three damp boggy localities with rank herbage. No post-larval stages known.

O'Mahony, E. (1946). 'Records of Trichodectidae (Mallophaga).' Ent. Mon. Mag. 82: 211.

Host records of *Trichodectes melis* on badger, with stray records on dog and marten; *Stachiella mustelae* on weasel; *S. erminea* from stoats; *Bovicola bovis* from ox; *B. equi* from ass; and *Felicola subrostrata* from wild cat.

Phillips, S. M. (1946). 'Occurrence of nematodes in a collembolan.' Ent. Mon. Mag. 82: 218–19.

A specimen of *Neanura grassei* captured near Feock, Cornwall, contained parasitic nematodes and differed from the type in being a third as long again and lacking the characteristic reticulations on the body.

Prentice, I. W. & Harris, R. V. (1946). 'Resolution of strawberry virus complexes by means of the aphis vector *Capitophorus fragariae* Theob.' Ann. Appl. Biol. 33: 50–3.

A biological method of separating component viruses from mixtures in strawberry plants.

Turk, F. A. (1946). 'The Siphonaptera of Cornwall and the Isles of Scilly with the description of a new subspecies.' Ent. Mon. Mag. 82: 97–100.

A list of 23 species of fleas mainly on mammals and from birds' nests. *Ceratophilus columbae*, *C. fringillae* and bat fleas are very rare. Detailed notes are given of the hosts, location, abundance and distribution. *Palaeopsylla minor cornubiensis* n.subsp. is described and is intermediate between British *P. minor* and Spanish *P. iberica*.

Turk, F. A. & Phillips, S. M. (1946). 'A monograph of the slug mite—*Riccardoella limacum* (Schrank).' Proc. Zool. Soc. Lond. 115: 448–72.

Systematics, anatomy, reproduction and general habits of this species. The fully adult form is in process of disappearing from the life cycle and a nymphal stage is mainly the reproductive one. A number of observations on the habits of these mites in relation to their hosts are given, e.g. the method of finding them by following the slime trail.

Webb, J. E. & Harbour, H. E. (1946). 'Occurrence of foot louse of sheep in the British Isles.' Nature, Lond. 158: 587.

The first known occurrence of the sucking louse *Linognathus pedalis* in the British Isles was recorded in June 1946 near Colchester, Essex.

4. FOOD AND FOOD HABITS

Allan, P. B. M. (1945). 'Food plants of *Saturnia pavonia* L.' Northw. Nat. 20: 260.

The larvae of this moth are recorded feeding on *Rhamnus catharticus* and *Poterium sanguisorba*.

Bretherton, R. B. (1946). 'Some "clearwings" in the Oxford district.' Ent. Mon. Mag. 82: 213–17.

Detailed notes on the distribution, habitats and life history of *Aegeria formiciformis* (osier stumps), *A. culiciformis* (birch stumps), *A. vespiformis* (oak stumps), *A. tipuliformis* (blackcurrant stems), *A. flaviventris* (galls of *Salix cinerea*), *A. andreniformis* (*Viburnum lantana* stems), *Trochilium apiformis* (black poplar), *T. crabroniformis* (old stems of *Salix caprae*) and more rarely, *A. ichneumoniformis* (*Lotus corniculatus*) and *A. myopaeformis* (apple trees).

Campbell, J. W. (1946). 'The food of the wigeon and brent goose.' Brit. Birds, 39: 194–200, 226–32.

A preliminary account giving the results of 'stomach' analyses of 344 wigeon (*Anas penelope*) and 28 brent geese (*Branta bernicla*). In the former species an intensive investigation of an area in N. Uist included a survey of the availability of the various food plants. Wigeon in this locality preferred *Ruppia* to *Zostera*, and it seems likely that their distribution and numbers are not dependent on the latter plant, as has been surmised. Data from other areas, though not supported by surveys, show that various algae, salt-marsh plants and grasses may at certain times and places be the predominant foods.

Campbell, J. W. (1946). 'Notes on the food of some British birds.' Brit. Birds, 39: 371–3.

Notes on the 'stomach' contents of the following species are given: 3 starlings (*Sturnus vulgaris*); 3 stonechats (*Saxicola torquata*); 2 redshank (*Tringa totanus*); 13 barnacle geese (*Branta leucopsis*); 23 golden plover (*Charadrius apricarius*); and 3 red grouse (*Lagopus scoticus*). All were collected in N. Uist, Outer Hebrides.

Chambers, V. H. (1946). 'An examination of the pollen loads of *Andrena*: the species that visit fruit trees.' J. Anim. Ecol. 15: 9–21.

A technique for the examination of individual pollen loads collected by bees of the genus *Andrena* is described, and its application in the study of the foraging behaviour of these insects is illustrated and discussed. Observations of the flight periods of *A. varians*, *haemorrhoa*, *armata* and *pubescens*, in relation to the flowering of cultivated and native forms of *Prunus* and *Pyrus* in the years 1941–5 are given. The results of quantitative analyses of pollen species in the loads show that *A. varians* has a definite preference for fruit-tree pollen, whereas the other three species of *Andrena* considered do not show the same high degree of preference.

Collinge, W. E. (1945). 'The effect of nutrition on the sex ratio of terrestrial Isopoda.' Northw. Nat. 20: 261–2.

When *Armadillidium vulgare* was reared in captivity on a highly nutritive diet, all the individuals of 11 broods and 85% of another six were females, but when the diet was poor and scanty all the individuals of five and most of those of two broods that received it were males. Somewhat similar results were obtained with *Oniscus asellus*, *Philoscia muscorum* and *Porcellio scaber*.

Colquhoun, M. K. (1946). 'Wood-pigeons and agriculture.' J. Minist. Agric. 53: 181–4.

Includes annual food cycle, effect of weather and flocking.

Cooper, B. A. (1946). 'The habitat of *Limonius minutus* L. (Col., Elateridae).' Ent. Mon. Mag. 82: 148–51.

Limonius minutus is associated with the presence of fungus mycelium in the soil (as in fairy rings). The soil in such areas is always dry and friable. *Corymbites nigricornis* (=*C. incanus* of Van Emden's key, 1945, Ent. Mon. Mag. 82: 128) is not fungivorous, but a normal soil feeder.

Duffy, E. A. J. (1946). 'Records of coleopterous larvae from Surrey with a note on host-plants.' Ent. Mon. Mag. 82: 270–3.

Detailed notes on the ecology and larval development of 27 species of beetle larvae including *Synchita humeralis* (Colydiidae), *Pediacus dermestoides* (Cucujidae), *Cardiophorus asellus* (Elateridae), and *Hallomenus binotatus* (Synchroidae), together with a list of host plants for 13 wood-feeding beetles.

Frost, W. E. (1946). 'Observations on the food of eels (*Anguilla anguilla*) from the Windermere catchment area.' J. Anim. Ecol. 15: 43–53.

The stomach contents of 106 yellow eels from Windermere, 42 from Cunsey Beck and 32 from the River Leven were examined; the food of 60 seaward migrating eels caught in the trap at Cunsey Beck was also ascertained.

Eels feed almost entirely upon bottom-living invertebrates, molluscs predominating in the Windermere samples and larvae of aquatic insects in those from Cunsey and Leven. This distinction may be due to the difference in size of the eels examined from the two places and the difference in faunistic conditions there. A negligible number of Windermere eels feed on fish; the virtual absence of fish from the diet of the other eels may be due to the size of those examined. Some seaward migrating eels, both wholly silver and those changing from yellow to silver, contained food. The relationship between the feeding habits of the eel and fish associated with it is discussed, and some suggestions for fishery policy based on this are put forward. The internal parasites found are mentioned. Seven tables of food organisms are given.

Jones, N. S. (1946). 'Browsing of *Patella*.' Nature, Lond. 158: 557–8.

The browsing of the limpet *Patella vulgata* is of importance in foreshore ecology; algae such as *Enteromorpha compressa*, *Porphyra umbilicalis* and *Ulva linza* were removed before they could become established in a cleared area.

Lumsden, W. H. R. & Haddow, A. J. (1946). 'The food of the shag (*Phalacrocorax aristotelis*) in the Clyde sea area.' J. Anim. Ecol. 15: 35–42.

The stomach contents of 81 shags (78 from the Firth of Clyde) were examined. The diet consisted largely of fish. 900 fish, belonging to at least 20 species, were found. Crustacea were often found in the stomachs of shags from certain areas. Large annelids were found, but were never common. Remains of a squid were recovered from one stomach. Large numbers of fish otoliths were found, counted, and identified where possible. Feeding habits of the shag were studied in nature. The conclusion is that the shag feeds mainly on fish of no commercial value and does negligible damage to food-fish. Four tables of stomach contents from shags shot in different localities are given, and a table and diagram give the percentage of various food organisms found. A new record for the Clyde area of the prawn *Leander serratus* is given.

Moreton, B. D. (1946). '*Baris laticollis* Marsh. (Col., Curculionidae), a pest of *Brassica* crops.' Ent. Mon. Mag. 82: 274–5.

Originally local and feeding on roots of *Sisymbrium officinale*, this species has begun to attack *Brassica* crops at Brighton, Sussex, and Ipswich, Suffolk. Life history: adults emerged in late summer, feed on cabbage stems, retire into the soil during the winter, emerge in spring and begin to drill holes in the stems and to perforate the leaves. The eggs are laid near the base of the stem in early summer. The larvae mine the tap root and stem base but do not form galls. Pupation and emergence of adults takes place in the early autumn. A small proportion of larvae overwintered.

Richards, O. W. (1946). 'Rearing larvae of the eyed hawk moth, *Smerinthus ocellatus* (L.) (Lep., Sphingidae), on apple and sallow.' Proc. R. Ent. Soc. Lond. A, 21: 72.

Larvae fed on sallow, produce more pellets than those fed on apple.

Wakely, S. (1945). 'Notes on the genus *Mompha*.' Proc. S. Lond. Ent. Soc. 1944–5: 81–4.

Mentions 13 species of these Tineoid moths and their food plants.

5. POPULATION STUDIES

Alexander, W. B. (1946). 'The index of heron population, 1945.' Brit. Birds, 39: 201–4.

This yearly sample survey showed that in 1945 over England and Wales the population of herons (*Ardea cinerea*) was about the same size as in 1944, though the Midlands and north-west of England showed a distinct decrease. The trends since 1938 are compared graphically with mean temperature for the coldest month at two localities. A supplementary note (pp. 204–6) by D. Lack entitled 'The balance of population in the heron', draws attention to the rapid return to par of the heron population after a severe winter, and suggests that an increased proportionate number of mature birds survive during the winter after a severe spell, and so bring back the numbers quickly.

Barker, A. Neville (1946). 'The ecology and function of Protozoa in sewage purification.' Ann. Appl. Biol. 33: 314–25.

Fluctuations of the population are limited by different factors in different seasons.

Broadbent, L. (1946). 'Note on the effect of wireworms of the genera *Agriotes* and *Corymbites* on crop yields.' Ann. Appl. Biol. 33: 166–9.

Illustrates the regular falling off of yield of crops due to increasing wireworm populations under controlled conditions.

Brown, F. J. (1946). 'A Cheshire starling roost, 1944–5.' J. Anim. Ecol. 15, 1: 75–81.

The times of dispersal and assembly relative to sunrise and sunset respectively, of a roost of starlings (*Sturnus vulgaris*), near Crewe, showed seasonal variation. The duration of communal flight and assembly also varied with the time of the year, both being curtailed or dispensed with in mid-winter. Definite flight lines were regularly used, but by varying numbers of birds, showing that some of them changed their feeding grounds from time to time. Preliminary assembly often took place at remote points. Birds going to distant feeding grounds dispersed first and returned late during assembly, thus spending little less time at their feeding grounds than those not going so far. Starlings occupied one part of the wood and other species of birds used the remainder without any sign of hostility.

Brown, P. E. (1946). 'Preliminary observations on a colony of reed-warblers.' Brit. Birds, 39: 290–308.

Detailed and critical notes on a colony of reed warblers (*Acrocephalus scirpaceus*), whose maximum numbers were about 15 pairs. Arrival of birds extended over 3–4 weeks, and territories varied between 60 and nearly 500 sq.yd. with some overlap. Detailed notes on nest building, clutch size, incubation, song and other points of biological interest.

Ellison, N. F. (1945). 'Increase of seals in the Dee Estuary.' Northw. Nat. 20: 268.

Seals have increased considerably in the Dee Estuary since 1910, and during 1941–5, 4–12 were present in most months of the year. On 24 August 1945 a herd of 32 common seals (*Phoca vitulina*) was observed. Grey seals (*Halichoerus grypus*) also occurred in the estuary.

Elton, C. (1946). 'Competition and the structure of animal communities.' J. Anim. Ecol. 15: 54–68.

An analysis of the published ecological surveys of 55 animal (including some parasite) communities and 27 plant communities from a wide range of habitats, and the frequencies of genera with different numbers of species tabulated. A rather constant and high percentage of genera with only one species present was found, the average being 86% for animal and 84% for plant communities. The corresponding average numbers of species per genus were 1·38 and 1·22. These figures differ considerably from those of a faunal list for any large region: the percentage of genera with only one species present for eleven large British insect groups is 50, and the average number of species per genus is 4·23. This difference in frequency is attributed to existing or historical effects of competition between species of the same genus. These conclusions apply at present only to the list of communities hitherto studied with any completeness; the animal communities analysed are mostly ones in which the primary consumer species depend on only a few natural resources. The important problem of how certain groups of species (mostly separated by generic factors) are able to exist together in the same area, drawing on a common pool of resources, remains to be solved.

Fitter, R. S. R. (1946). 'Report of the black redstart inquiry for 1945.' Brit. Birds, 39: 207–11.

Collected observations show that this newly established species (*Phoenicurus ochrurus*) was recorded as present slightly less frequently in 1945 than in 1943 and 1944.

Korringa, P. (1946). 'A revival of natural oyster beds?' Nature, Lond. 158: 586–7.

Failure to revive the once-prolific oyster beds of western Europe has been ascribed to the lack of suitable mother-oysters. The author considers that the reproductive powers of *Ostrea edulis* are being over-rated, and gives data collected in the Oosterschelde to support this theory. The importance of providing cultch material is stressed.

Lack, D. (1946). 'Do juvenile birds survive less well than adults?' Brit. Birds, 39: 258–64.

An analysis of the distribution of recoveries of marked birds shows that for common species such as the blackbird (*Turdus merula*), the song thrush (*T. ericetorum*), the starling (*Sturnus vulgaris*) and the lapwing (*Vanellus vanellus*), the proportional mortality is higher in the 12 months starting on 1 August after fledging than in the 12 months starting 1 November after fledging or on any later date. Thus there is a higher rate of dying among birds up to about four months old than among older ones, and this cannot be explained by bias in the recovery figures.

Leslie, P. H., Perry, J. S. & Watson, J. S. (1946). 'The determination of the median body-weight at which female rats reach maturity.' Proc. Zool. Soc. Lond. 115: 473–88.

Taking samples of female rats of two species, *Rattus norvegicus* and *R. rattus*, in groups of equal weight, the probits corresponding to the percentage of each sample that had reached maturity (the presence of corpora lutea indicated this) were found to have a straight-line relationship with the logarithm of body weight. This was checked against a small sample of 27 rats, in which histological investigation showed that the first ovulation had just occurred and the correspondence was satisfactory. This method therefore enables the onset of maturity to be compared between different species or samples of the same species.

MacLagan, D. S. (1941). 'Recent animal-population studies; and their significance in relation to socio-biological philosophy (Part 1).' Proc. Univ. Durham Phil. Soc. 10: 310–31.

A number of experimental studies by different workers using protozoans and insects, on the effects of density on animal populations, are discussed. They show that there is an optimum density for various physiological processes which concern the reproductive rate, growth and longevity of populations. The adverse effects observed due to overcrowding are also discussed.

Orton, J. H. (1946). 'Survival of oyster and other littoral populations.' Nature, Lond. 158: 586.

Discusses some of the factors influencing survival of populations of *Ostrea edulis*; the removal of all larger oysters from the beds, and the reduction in the number of scattered small plots cultivated reduces the chance of survival. It is still not known whether cross-fertilization occurs.

Parkhurst, R. & Lack, D. (1946). 'The clutch-size of the yellow-hammer.' Brit. Birds, 39: 358–64.

Two sets of data are given. The first, from a single area of Oxfordshire during a single season shows that the clutch-size of this species (*Emberiza citrinella*) increases from a mean of 3·5 to 3·9 from mid-May to the end of June and declines after this to 2·7. The second set of data from various localities in England over a period of years shows the same trend but with fewer irregularities, since there is also variation from year to year. Data for hatching success show that it increases as the season progresses.

Perry, J. S. (1945). 'The reproduction of the wild brown rat (*Rattus norvegicus* Erxleben).' Proc. Zool. Soc. Lond. 115: 19–46.

A detailed investigation carried out upon samples from urban and rural habitats. All aspects of reproduction are dealt with quantitatively and histological routines were used to determine, e.g. numbers of corpora lutea and presence of unimplanted stages. Breeding was found to be continuous throughout the year, with a peak from April to June. The examination of bodies suggested that each female has a period of intensive breeding during which litter follows litter, and then a period of quiescence. Fertility, as indicated by the number of ovulations, varied with the body weight of the female, and intra-uterine mortality was distributed at random over the stages of gestation (in contrast to what happens in the rabbit) and totals some 25%.

Reynolds, R. A. W. (1946). 'Variations in clutch size and some nesting success data.' Brit. Birds, 39: 337–9.

Observations on nests of the blackbird (*Turdus merula*) and song thrush (*T. ericetorum*) show that the mean clutch size tends to increase as the nesting season progresses. Hatching and fledging success data are given for several common species.

Richards, O. W. (1946). 'Observations on *Bombus agrorum* (Fabricius) (Hymen., Bombidae).' Proc. R. Ent. Soc. Lond. A, 21: 66–71.

The number of larvae attended by known numbers of workers. Queens can best be separated from workers by weighing them. Old worn workers are smaller and lighter than fresher ones, while foragers are larger than workers found in the nest.

Salt, G. & Hollick, F. S. J. (1946). 'Studies of wireworm populations. II. Spatial distribution.' J. Exp. Biol. 23: 1–46.

Wireworms (*Agriotes* spp.) are not distributed at random in a field, but are markedly aggregated, this being largely due to the small individuals. Wireworm distribution is highly correlated with certain soil factors, type of vegetative cover and predacious animals.

Shorten, M. R. (1946). 'A survey of the distribution of the American grey squirrel (*Sciurus carolinensis*) and the British red squirrel (*S. vulgaris leucourus*) in England and Wales in 1944–5.' J. Anim. Ecol. 15: 82–92.

Analysis of a questionnaire survey covering 9495 parishes. Forestry Commission areas in Scotland and public parks in London and 15 big towns and cities are also covered by the survey. The grey squirrel is found to have increased its range since the last survey in 1937; it is now present in 112 new squares of a ten-kilometre grid on the western boundary of its range. The red squirrel is more widely and thinly distributed than the grey. 1123 parishes contain both species; but 66% of the squares occupied by the grey squirrel in 1930 now report no red squirrels. The survey covers an area of 15,800 square kilometres, and was carried out with the help of the War Agricultural Executive Committees. There are five maps in the text.

Shorten, M. R. (1946). 'The distribution of the grey squirrel (*Sciurus carolinensis* Gmelin) and the British red squirrel (*S. vulgaris leucourus* Kerr) in Lincolnshire.' Trans. Linc. Nat. Union, 11: 108–14.

Results of the inquiry into the distribution of these two species for 260 parishes in Lincolnshire, during the period 1944–5.

Singh, B. N. (1946). 'A method of estimating the numbers of soil Protozoa, especially amoebae, based on their differential feeding on bacteria.' Ann. Appl. Biol. 33: 112–18.

Thomas, D. C. (1946). 'A study of the distribution of the swede midge (*Contarinia nasturtii* Kieffer) in Devon and symptoms of its attack on various host plants.' Ann. Appl. Biol. 33: 77–81.

Incidence of attack on cow cabbage is most severe in the north and west of Devon, while attack on swedes is heaviest in the south and east.

Wattison, J. T. (1945). 'Unusual abundance of burnet moths.' Northw. Nat. 20: 260.

Large numbers were seen on 8 July 1945 near Much Wenlock, Salop. *Zygaena lonicerae* and *Z. filipendulae* were present in approximately equal numbers, mostly feeding at *Centaurea nigra*. No moths were seen 3 weeks later.

Wilson, G. Fox- (1946). 'Factors affecting populations of social wasps, *Vespula* species, in England (Hymenoptera).' Proc. R. Ent. Soc. Lond. A, 21: 17–27.

Effect of spring rainfall, spring, autumn and winter temperatures, humidity, available food, e.g. aphides, and of natural enemies upon the abundance of wasps at Wisley, 1921–45.

Wright, D. W. & Ashby, D. G. (1946). 'Bionomics of the carrot fly (*Psila rosae* F.) I. The infestation and sampling of carrot crops.' Ann. Appl. Biol. 33: 69–77.

The pattern and intensity of carrot fly attack in a field is largely determined by the degree, position and suitability of the adjoining shelter.

Wright, D. W. & Ashby, D. G. (1946). 'Bionomics of the carrot fly (*Psila rosae* Fab.) II. Soil populations of carrot fly during autumn, winter and spring.' Ann. Appl. Biol. 33: 263–70.

The winter is passed both in the puparial and larval stages. Many of the larvae complete their development during the winter. Mortality during the winter varies considerably but never appears to be sufficiently high to imperil the survival of the population. A Braconid, *Dacnusa gracilis*, a Proctotrupoid Diapriid, *Loxotropa tritoma*, and the Staphylinid beetle *Aleochara sparsa*, as well as fungi, bacteria and nematodes attack the overwintering population.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Adams, C. V. (1946). 'A method of marking insects.' Entomologist, 79: 169–71.

Discusses methods of marking Lepidoptera and describes a modification of Fletcher's method which was used with success upon *Aglais urticae*. An area on the wing is freed from scales by means of cotton wool and a $\frac{3}{16}$ in. label of transparent paper stuck on with seccotine. For local experiments this label to bear a number written in waterproof ink and corresponding with notebook entries. Larger Diptera and dragonflies were marked by applying small drops of molten wax crayon by means of an electrically heated needle. The six colours red, yellow, blue, green, black and brown, applied in pairs, yield 31 distinctive combinations of colours, if confusing pairs (e.g. red and brown) are avoided. These combinations are sufficient to indicate the date on one wing and the month on the other.

Anon. (1946). 'Colorado beetle in England in 1945.' J. Minist. Agric. 53: 129–33.

In addition to the occurrence of occasional beetles on boats and single beetles at three places near English ports, small outbreaks were discovered at Faversham (Kent), in the Deal (Kent)–Ramsgate (Kent)–Worthing (Sussex) areas and Minsterworth, Gloucestershire.

Broadbent, L. (1946). 'Alate aphides trapped in north-west Derbyshire, 1945.' Proc. R. Ent. Soc. Lond. A, 21: 41–6.

Analysis of 2560 aphides belonging to at least 62 species caught between early May and mid-November 1945 on six sticky traps, three of which were at or more than 1000 ft. above sea level and three between 340 and 460 ft. above sea level.

Carlström, D. & Edelstam, C. (1946). 'Methods of marking reptiles for identification after recapture.' Nature, Lond. 158: 748–9.

A photograph of the ventral pattern of the grass-snake (*Natrix natrix*) is a permanent means of identification.

Dannreuther, T. (1946). 'Migration records, 1945.' Entomologist, 79: 97–110.

This year was remarkable for invasions of Bath whites (*Pontia daplidice*) and long-tailed blues (*Lampides boeticus*), but most migrants were exceptionally abundant. Detailed notes of the course of invasion and abundance of the main migrants: *Vanessa cardui, V. atalanta, Colias croceus, C. hyale, Pieris brassicae, Acherontia atropos, Herse convolvuli, Macroglossum stellatarum, Plusia gamma, Nomophila noctuella* and 32 other species of rare Lepidopterous immigrants, together with 9 species of other orders.

Dannreuther, T. (1946). 'Records of the Bath white butterfly (*Pontia daplidice*) (L.) observed in the British Isles during 1945.' J. Soc. Brit. Ent. 3: 1–7.

650 Bath whites were seen in 1945. 300 first brood and 100 second brood were captured. First recorded at Bournemouth, Dorset, on 12 July, and another large swarm seen near Looe, Cornwall, on 14 July. Limits of range were: West, Co. Kerry; north, Rutland; and east, at Walmer. A few wild larvae were found on *Reseda luteola* and *Sisymbrium officinale*. This unprecedented invasion was associated with large numbers of other immigrant species, and may be correlated with severe drought in south-west Europe. Detailed notes of all known 1945 records are appended.

Dannreuther, T. (1946). 'Records of the long-tailed blue butterfly (*Lampides boeticus*) (L.) observed in the British Isles in 1945.' J. Soc. Brit. Ent. 3: 8–9.

From 1824 to 1939, only 32 British specimens have been recorded. 24 were recorded in 1939 and detailed notes of all known 1945 records are appended. Three individuals of the short-tailed blue (*Everes argiades*) were also captured. Only seven others have been recorded since 1874.

Dobson, R. & Lockley, R. M. (1946). 'Gannets breeding in the Channel Islands: two new colonies.' Brit. Birds, 39: 309–12.

Two colonies of *Sula bassana*, one of about 200, the other of about 250 pairs, have been found on stacks in the Channel Islands group. These were known to be uninhabited by gannets in 1940. The nearest established colony to these new ones is Grassholm, 195 miles away.

Ellison, N. F. (1945). 'Lesser octopus on Cheshire coast.' Northw. Nat. 20: 262.

A living, medium-sized female of the deep-sea species *Eledon cirrosa* on the shore at Caldy, West Kirby, in August 1945, and a dead specimen washed ashore several days later.

Fraser, F. C. (1946). 'What is the condition of an immigrant butterfly on its arrival in this country: fresh or worn?' J. Soc. Brit. Ent. 3: 10–13.

Butterflies newly arrived from migration over seas are not necessarily worn, particularly if they have only crossed the channel. Hence the capture of specimens in perfect condition need not imply that they have been bred in England. This is supported by the condition of the initial wave of *Pontia daplidice* and by a study of the records of *Pieris brassicae* and *Vanessa atalanta*.

Freeman, J. A. (1946). 'The distribution of spiders and mites up to 300 ft. in the air.' J. Anim. Ecol. 15: 69–74.

The distribution of spiders in the air up to about 300 ft. was investigated by trapping in nets flown from wireless masts at Tetney, Lincolnshire, during 1934 and 1935. The spiders, of which a full list is given, showed a fairly even distribution in the air, the majority being adult and immature Linyphiidae and the young stages of other families. The largest numbers of spiders were found in the air when the temperature was in excess of 64° F., the relative humidity below 60% and the wind velocity below 12 m.p.h., the last factor having apparently the greatest influence. The occurrence of mites, both free and on the bodies of insects, is also recorded.

Kettlewell, H. B. D. (1946). 'Female assembling scents with reference to an important paper on the subject.' Entomologist, 79: 8–14.

Female assembling scents in moths are apparently airborne, as is shown by the presence of an upwind zone of no attraction and the fact that the best conditions for assembling are dusk and dawn. Amputation of both male antennae in *Panaxia dominula* destroyed power of perception of attractive female scent; amputation of one antenna only destroyed power of perception of direction of scent. Benzene extraction of 34,800 ♀ genitalia of *Lymantria dispar* produced a substance which is a specific attractant for the male gypsy moth. This substance was further treated and isolated in a relatively pure state.

Kevan, D. K. (1946). '*Ips typographus* on imported German logs.' Ent. Mon. Mag. 82: 241.

A major European pest of spruce forests accidentally imported in German logs which were widely distributed in Great Britain. Severe infestation may arise.

Laurie, E. M. O. (1946). 'The coypu (*Myocastor coypus*) in Great Britain.' J. Anim. Ecol. 15: 22–33.

There are records of escapes of this South American rodent from fur farms in the southern and south eastern counties of England, and wild colonies of coypus are established at least in parts of east Norfolk, and on a sewage farm near Slough, Buckinghamshire. The coypus live along the banks of rivers and streams and in marshy land close to open stretches of water; the vegetation here (largely sedges, (*Carex* spp.) and reeds (*Phragmites communis*) provides cover as well as food. Stomachs of ten specimens showed an entirely vegetable diet. The weight of 84 animals caught in Norfolk ranged from 793 g. (1 lb. 12 oz.) to 8164 g. (18 lb.). There does not appear to be any marked difference in the reproductive rates of coypus living wild in Great Britain and those bred in captivity in Great Britain, or in South America, France or Russia. The first record for Great Britain of the louse *Pitrufquenia coypus*, before only recorded from its type locality in Chile, is given. Maps show the distribution of coypu fur farms in England, 1932–9; areas from which escapes have been reported; and the range of the species in 1944–5 along rivers in Norfolk.

Nowers, J. E. (1945). '*Macroglossa stellatarum* Linn.' Northw. Nat. 20: 260.

Fresh specimen of the humming-bird hawk moth captured on wallflowers at Darlington on 18 May 1945.

Tomes, G. A. R. & Brian, M. V. (1946). 'An electronic method of tracing the movements of beetles in the field.' Nature, Lond. 158: 551.

Describes the operation of a new form of Geiger-Müller tube which can detect the presence to within a few inches of Elaterid beetles (*Agriotes* Esch.) even when they are 4 in. below the soil. The beetles are first marked with radium sulphate deposited beneath the elytra between aluminium foil disks.

Went, A. E. J. (1946). 'Irish freshwater fish; some notes on their distribution.' Salm. Trout Mag., Lond. No. 118: 248–56.

Includes historical notes on the introduction of various species and calls attention to the uncertain status of various species of *Salvelinus*.

7. REPORTS OF ORGANIZATIONS

Éire, Department of Agriculture, Fisheries Branch (1946). Report on the sea and inland fisheries for the year 1945. Dublin, 28 pp. Price 9*d*.

The yield of salmon and trout was extremely low in 1945.

Freshwater Biological Association of the British Empire (1946). Fourteenth Annual Report for the year ending 31st March, 1946. 54 pp. (Price to non-members, 1*s*. 6*d*. F.B.A., Wray Castle, Ambleside, Westmorland.)

The Director's Progress Report gives at some length in non-technical language an account of biological and physico-chemical work in progress at Wray Castle. Particular mention should be made of the perch trapping experiment, an essay in population control, and of results of algological work.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1946

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance:		
Members taking *Journal of Ecology* only	324 11 7	
Members taking *Journal of Animal Ecology* only	209 5 6	
Members taking both Journals	187 18 4	
Associates	2 5 0	
	724 0 5	
Less Reserve allocated to 1946 vol. of *Journal of Ecology*, not yet published	304 0 0	
	420 0 5	
Add Reserve Bt. Fd. from 1945 for 2nd parts of both Journals	230 0 0	
		650 0 5
Interest on Investments	72 0 0	
Interest on Deposit Account	2 4 8	
Interest on P.O. Savings Bank Account	10 8 4	
		84 13 0
Journal of Ecology. Sales *less* Cost		283 10 5
Index to *Journal of Ecology*, vols. 1–20, Sales *less* Cost		2 11 9
		£1,020 15 7
Journal of Ecology:		
Sales: Balance of volume 33 (1945)		396 15 3
Back volumes and parts		398 5 4
Reprints of Papers		8 3 7
Overcharge of Insurance from 1945		1 9 5
		£804 13 7
Journal of Animal Ecology:		
Sales: Balance of volume 14 (1945)		145 5 4
Current volume 15, 2 parts (1946)		327 7 0
Back volumes and parts		276 9 10
Reprints of papers		53 15 0
Grant from H. R. Napp Ltd.		100 0 0
		902 17 2
Balance (see above, under Expenditure)		336 17 7
		£1,239 14 9

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Meeting expenses	31 6 1	
Printing and Stationery	12 13 11	
Travelling	12 11 6	
Clerical assistance	10 0 0	
Postages	9 6 8	
Audit Fee	6 6 0	
Bank Charges	1 0	
		82 5 2
Grant to Freshwater Biological Association		10 0 0
Subscription to Parliamentary & Scientific Committee		10 10 0
Journal of Animal Ecology. Cost *less* Sales		336 17 7
Biological Flora of the British Isles:		
Cost of Printing, Commission, etc.	156 2 2	
Less Sales of Reprints	35 17 3	
		120 4 11
		559 17 8
Balance—Surplus for the Year (To Balance Sheet)...		460 17 11
		£1,020 15 7
Journal of Ecology:		
Cost: Volume 33, Part 2		
Paper, Blocks, Printing and Binding ...		401 8 0
Publishers' Commission		97 11 4
Carriage, etc.		14 14 10
Editorial Expenses		5 14 0
Insurance of Stock		1 15 0
		521 3 2
Balance (see above, under Income)		283 10 5
		£804 13 7
Journal of Animal Ecology:		
Cost: Volume 14, Part 2		
Paper, Blocks, Printing and Binding ...	390 19 7	
Carriage, etc.	7 2 4	
		398 1 11
Cost: Volume 15		
Papers, Blocks, Printing and Binding ...	688 10 6	
Carriage, etc.	21 14 1	
Fee for checking references	10 0 0	
		720 4 7
Publishers' Commission		111 1 0
Insurance of Stock		10 7 3
		£1,239 14 9

BALANCE SHEET AT 31 DECEMBER 1946

Assets

	£ s. d.	£ s. d.
Cash in hand at Westminster Bank		
Current Account	189 3 2	
Deposit Account	550 0 0	
		739 3 2
Post Office Savings Bank Account		510 8 4
Publishing Accounts—Amounts due from Cambridge University Press:		
Journal of Animal Ecology	436 10 3	
Journal of Ecology	102 12 2	
Biological Flora of the British Isles	19 13 9	
		558 16 2
Investments at Cost:		
£1,200 of 3½% War Loan Stock	1,230 4 1	
£700 of 3% Savings Bonds 1960/70	700 0 0	
£300 of 3% Savings Bonds 1965/75	300 0 0	
		2,230 4 1
		£4,038 11 9

A further Asset, not valued, is the Unsold Stock of Journals, Index Volume and *Biological Flora* Reprints held by the Publishers for the Society.

VICTOR S. SUMMERHAYES
ALEX. S. WATT
Hon. Treasurers.

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1947		7 10 0
Library Fund		1 5 0
Printing Accounts due to the Cambridge University Press:		
Journal of Animal Ecology (3 Accounts)	341 10 3	
Journal of Ecology, Index Vols. 1–20	3 4 0	
		344 14 3
Subscription due to Parliamentary & Scientific Committee		10 10 0
Reserve of Subscriptions for 1946 allocated to *Journal of Ecology* for 1946, not yet published		304 0 0
General Revenue Account—Surplus in hand:		
Balance in hand 31 December 1945	2,909 14 7	
Surplus for 1946	460 17 11	
		3,370 12 6
		£4,038 11 9

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants.

120 BISHOPSGATE, E.C. 2
and
231*a* HIGH ROAD, LOUGHTON, ESSEX.
4 *June* 1947.